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Production of Juvenile Atlantic Salmon, *Salmo salar*, in Natural Waters

Edited by
R. J. Gibson and R. E. Cutting

Canada

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Abstract

Gibson, R.J., and R.E. Cutting [ed.] 1993. The production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118: 262 p.

This publication contains contributed papers and abstracts from presentations given at an international symposium held in St. John's, Newfoundland, June 25-27, 1991, hosted by the Department of Fisheries and Oceans, Government of Canada. The publication presents knowledge and research in progress in scientific fields related to natural production of juvenile Atlantic salmon and some other ecologically similar fluvial salmonids.

Résumé

Gibson, R.J., and R.E. Cutting [ed.] 1993. The production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118: 262 p.

Cette publication rassemble des articles et des résumés de communications présentés à un symposium international qui s'est tenu du 25 au 27 juin 1991 à St. John's (Terre-Neuve) sous le patronage du ministère des Pêches et des Océans, gouvernement du Canada. Elle fait le point sur les connaissances et les recherches en cours dans des domaines scientifiques liés à la production naturelle de saumon atlantique juvénile et d'autres salmonidés vivant dans les cours d'eau et présentant les mêmes charactéristiques sur le plan écologique.

Foreword and Acknowledgements

These Proceedings arise from a symposium held at Memorial University of Newfoundland, St John's, from June 25–27, 1991, and hosted by the Department of Fisheries and Oceans, Newfoundland Region. The purpose of the symposium was to assemble present knowledge and research in progress in scientific fields related to natural production of juvenile Atlantic salmon.

Increasing emphasis is being placed on the freshwater habitat and on production of juvenile Atlantic salmon, as controlling factors in the abundance of adult salmon. In the light of curtailments of the commercial salmon fisheries in Canada (with the consequent loss of statistics concerning adult fish), changes will occur in densities, production and life history strategies during the juvenile stages, which must be quantified in order to understand the results of, and make recommendations for, stock management. Techniques are needed to quantify productive capacity of the habitats, for enhancement, for restoration, and for conservation purposes, for assessment purposes in relation to the status of stocks, and for methods and validity of estimating smolt yields. Such an approach, based upon juvenile salmon, is the most practical and efficient way of providing production advice for management of adult Atlantic salmon. Management strategies have not always met with success, and we must know more about biological processes throughout the salmon's life history.

The three days of the symposium had six sessions, the final one being a synthesis. The five sessions at which papers were presented had the following themes:

(1) Stream ecology; invertebrates; predators.
(2) Habitat improvement; competitive effects; behaviour; dispersal.
(3) Habitat and production of juvenile salmon.
(4) Methods of evaluating standing stocks; relationships with productive capacity of the habitat for juvenile salmon.
(5) Population dynamics; relationships of juvenile salmon estimates to smolt yield.

Thirty-six papers were presented. In addition, eleven presentations were made at the poster session.

Chairmen of the six sessions, in sequence, were: R.J. Gibson; L.H. Bain; E.M.P. Chadwick; T.G. Heggberget; T.R. Porter; and R.E. Cutting.

The symposium brought together leading scientists in the salmonid field. Papers and ensuing formal and informal discussions were conducive to personal interactions and stimulus to research that such international gatherings allow. Eminent keynote speakers presented appropriate papers to open four of the sessions. These scientists were (session in parentheses): (1) T.F. Waters; (3) J.M. Elliott; (4) G. Power; (5) G.J.A. Kennedy. Applied and basic research papers were presented on stream ecology, behaviour, physiology, competition, predation, and population dynamics. The diversity of presented papers reflects the diversity of problems involved in the ecology of fluvial salmonids and emphasises the importance of studying both biotic and abiotic factors of the ecosystem. The unique work of J.M. Elliott confirms the need for long-term studies to understand processes in population dynamics of stream salmonids.

The majority of speakers submitted manuscripts, which are published in the sequence of the general themes of the sessions. Abstracts only were submitted in some cases, and these are published after the manuscripts. We expect this publication to be a useful reference for anyone interested in natural production of salmon.

Social events and field trips were pleasurable, although the local field trips did nothing to dispel the myth that it is always foggy in Newfoundland. Nevertheless Tom Waters was heard to remark that he would have been disappointed if he had come to Newfoundland and not seen fog. Mike Chadwick's trip to Western Arm Brook on the west coast of the island was more successful; at least his group was able to see the scenery.

The organizing committee of the Department of Fisheries and Oceans consisted of: L.H. Bain, Ottawa; E.M.P. Chadwick, Moncton; R.E. Cutting, Halifax; R.J. Gibson (Chair), St John's; and T.R. Porter, St John's. The Regional Director of Science, Newfoundland Region, L.W. Coady, strongly supported this symposium and has made possible publication of these Proceedings. Financial support was also provided by J.S. Loch, Regional Director of Science, Gulf Region. Success of the symposium was due primarily to the participants themselves. We are grateful to the referees for their careful work in reviewing the manuscripts. The symposium could not have gone smoothly without the effective support of a large number of persons from the Department of Fisheries and Oceans and from Memorial University.

R.J. Gibson and R.E. Cutting (Editors)

Dynamics in Stream Ecology

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WATERS, T. F. 1993. Dynamics in stream ecology, p. 1–8. *In* R. J. Gibson and R. E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

Our understanding of dynamics in stream ecology has been greatly advanced over the past quarter century. This progress includes advances in secondary production, allochthony at the primary producer level, nutrient and elemental transport, invertebrate drift, and other subjects. Stream ecosystem theory was much enhanced with development of the holistic view of the catchment as the ecosystem, macroinvertebrate functional analysis, and the River Continuum Concept. Whereas advances were most relevant to trophic ecology and productivity of the benthos, severe problems exist at the next higher trophic level, i.e., trophic ecology of fishes (e.g., the Allen Paradox). There is need to place greater emphasis on allochthony at the secondary producer level (hyporheos, terrestrial invertebrates, snag habitat, etc.), as well as further need to integrate these potential fish-food resources and fish productivity into current stream continuum theory.

Notre connaissance de la dynamique de l'écologie lotique a fait de très grands progrès au cours du dernier quart de siècle. Les connaissances ont notamment avancé en ce qui concerne la production secondaire, l'allochtonie au niveau de la production primaire, le transport de nutriants et des minéraux, la dérive des invertébrés, entre autres sujets. La théorie de l'écosystème lotique a été enrichie par l'élaboration d'une vue globale du bassin versant comme écosystème, par l'analyse fonctionnelle des macroinvertébrés et par le concept du continuum lotique. Si l'avancement des connaissances était extrêment pertinent en ce qui concerne l'écologie trophique et la productivité du benthos, de graves problèmes se posent au niveau trophique suivant, c'est-à-dire l'écologie trophique des poissons (p. ex. le paradoxe d'Allen). Il est nécessaire d'accorder davantage d'attention à l'allochtonie au niveau des producteurs secondaires (hyporhéos, invertébrés terrestres, habitat de cache, etc.) et il faut poursuivre les travaux pour intégrer ces ressources alimentaires potentielles des poissons et la productivité des poissons dans la théorie actuelle du continuum lotique.

Introduction

Much progress has been made in the discipline of stream ecology over the past quarter century. Perhaps the greatest advance has been made in the area of dynamics, which comprises rates of change within or related to the stream ecosystem (Barnes and Minshall 1983a; Minshall 1988). Such changes, directly or indirectly, include the transfer of energy into, through, or out of the ecosystem. Examples of dynamics are food consumption and growth rates, transfer of organic matter into or out of the stream, production rates, and succession. Dynamics may be contrasted with the purely descriptive aspects of natural history, emphasized in an earlier scientific era, such as species lists, organism morphology, and abundance. Stream ecology dynamics are fundamental to fish production.

The term "production" in the title of this symposium may be used in two different ways: (1) the number and size of Atlantic salmon (*Salmo salar*) smolts "produced" by a year class and available for migration to the sea, and (2) total tissue elaboration by the entire population or year-class, whether surviving to the smolt stage or not, usually expressed in units of kilograms per hectare per year (wet mass), sometimes called "biological production". Both uses have important roles in fisheries, but each use must be clearly defined to avoid confusion between the two different concepts.

In 1970, H.B.N. Hynes's *The Ecology of Running Waters* was the definitive work in stream ecology, setting out the state of knowledge in the discipline at the time. For the past 20 years, this book has been the only single-volume treatment available in the subject of stream ecology in its entirety, and it seems highly improbable that a single volume could be similarly produced today. Yet, in 1970, *The Ecology of Running Waters* lay merely at the brink of knowledge in stream dynamics. The book gave us only a brief introduction to what lay soon ahead in progress in areas such as secondary production; nutrient transport; predator-prey relationships; invertebrate drift; food consumption and growth rates for both fish and invertebrates; allochthony; and many others. Hynes makes many statements about the inadequacy of available data and the incomplete solutions to problems of dynamics.

Theory development in stream ecology over these past twenty years has been exceptional. A few of the books and symposia published in this period include Ward and Stanford (1979), Barnes and Minshall (1983b), Fontaine and Bartell (1983), Resh and

Rosenberg (1984), Swank and Crossley (1988), and the symposium of the North American Benthological Society (1988). This review depends heavily, though not solely, upon these publications.

The field of stream ecology has fallen roughly into two major interest groups: (1) those aspects dealing with productivity of the ecosystem most relevant to the macroinvertebrate benthos, and (2) those aspects dealing mainly with the more applied interests in fisheries. Too often, it seems, the two areas have developed in isolation. The two groups of animals are usually the most obvious of the stream biota, and both are important as major elements affecting, and affected by, basic stream ecology. Thus, closer communication between the two interests appear to be called for, and it is one of the objectives of this paper to urge such an amalgamation.

Objectives of this paper are three-fold: (1) to briefly review some of the major issues in stream ecology, with emphasis on aspects of dynamics that would appear to have the greatest influence upon the subject of this symposium namely, the production of juvenile Atlantic salmon; (2) to discuss one of the major discrepancies in research results between benthos and fish biology, the Allen Paradox; and (3) to suggest possible resolutions to the Allen Paradox by interjecting a greater role of fishes in stream ecology theory. No inclusion of new research results is intended.

Major Issues in Stream Dynamics

Many subjects involving dynamics have received major attention since Hynes's (1970) treatise. The following short list reflects the author's judgment as ones attaining substantive progress, without implying inferior status to any others.

1. Secondary production. Great advances have been made over the past two decades in the methodology for estimating annual biological production by both invertebrates and fishes. Early methods proposed by Ricker (1946) and Allen (1949) using instantaneous growth rates have been in wide use for fishes; and original methods based on cohorts have been improved for invertebrates, such as the increment-summation (Kajak and Rybak 1966) and the removal-summation methods (Winberg 1971); the size-frequency method for invertebrates, which does not require the identification of a cohort, was initially proposed by Hynes (1961) and later improved and corrected by Hynes and Coleman (1968), Hamilton (1969), and Benke (1979), and is now in wide use. A large bank of data on production by stream benthos and fishes is available (especially for salmonids, *see* Elliott, this volume, for his 25–year record of brown trout (*Salmo trutta*) production). Major reviews on secondary production include those by Waters (1977), Benke (1984), and Downing and Rigler (1984), which includes much information published in the past 20 years.

2. Allochthony. Perhaps the greatest advance in stream ecology dynamics has been in the appreciation, experimentation, and theory of allochthony and detritus dynamics — wherein much of the energy driving the stream system originates in areas outside the stream channel. Whereas *The Ecology of Running Waters* included some of the pioneer work on this subject, an enormous amount of work on allochthony was accomplished after its publication (e.g., Kaushik and Hynes 1971; Cummins 1973, 1974; Wallace et al. 1977; Anderson and Sedell 1979; Cummins and Klug 1979; Wallace and Merritt 1980; Merritt and Wallace 1981). Most research, either directly or indirectly, has related to the invertebrate benthos, for which allochthonous energy is provided in the form of deciduous leaves and other organic matter of many kinds. Sizes of organic particles studied have ranged from dissolved organic molecules (Lush and Hynes 1978; Meyer et al. 1988b) to large woody detritus (Anderson et al. 1978; Webster and Benfield 1986). The role of bacteria and especially fungi in converting the allochthonous energy of plant detritus into nutritious food matter for invertebrates has been an important element of allochthony (Kaushik and Hynes 1971; Barlocher 1985).

In addition to the emphasis on the macroinvertebrates' food and energy source, the appreciation of allochthony also led to the holistic view — that is, that the entire catchment must be considered as the basic stream ecosystem (Townsend 1980; Minshall et al. 1983). The appreciation of allochthony also resulted in the functional group analysis, so elegantly put forward by Cummins (1974). That contribution brought order to the functional aspects of the benthic invertebrate community and to its use of food materials. Similarly, an appreciation of allochthony led to the River Continuum Concept (Cummins 1977; Vannote et al. 1980; Minshall et al. 1985), which refined and expanded older European schemes of river zonation (Huet 1959; Illies and Botosaneanu 1963). The concept has not been without its critics, especially in regions outside the North American temperate zone (e.g., Statzner and Higler 1985). But the basic concept of a predictable downstream succession, allowing for similarly predictable exceptions of climate and catchment type, was a major advance in stream theory. The concept essentially serves as a paradigm of theoretical framework against which existing streams and specific reaches may be evaluated (Minshall et al. 1985).

3. Nutrient and element transport. Movement of nutrients into and within a stream ecosystem was discussed by Hynes (1970). The quality and quantity of elements in stream water has long been considered to be the direct result of edaphic factors in the catchment. Recent studies (Elwood et al. 1981; Meyer et al. 1988a) have emphasized quantification of the sources, rates of transport, fate of elements, and dissolved inorganic and organic nutrients and have thus brought into sharper focus the catchment-as-ecosystem concept.

New concern and research includes evaluating the effects of disturbance resulting from dams, forestry and agricultural practices, and urbanization (Hannan 1979; Webster and Patten 1979). The concept of "spiraling" (Webster 1975; Elwood et al. 1983) views the cycling of nutrients and elements in a downstream direction, combining traditional views of biogeochemical cycles with the continuum concept. Recent studies also have emphasized the removal of energy from the stream by emerging aquatic insects (Jackson and Fisher 1986).

4. Invertebrate drift. Early work on stream invertebrate drift (Muller 1954; Waters 1962; Elliott 1965; and reviewed by Hynes 1970) stimulated a multitude of studies worldwide (see reviews by Waters 1972; Muller 1974; Wiley and Kohler 1984; Brittain and Eikeland 1988). Data on many aspects of drift proliferated in the literature during the past two to three decades. Most published data have been descriptive or have concentrated on causative factors that influence diel and seasonal variations. Specific concerns have been with the biorhythms involved (Muller 1974); relationships to fish feeding (Elliott 1970; Allan 1983); and to the large quantities involved prompting concern over the need for compensating upstream migration (Muller 1954, 1974; Hultin et al. 1969); the excess production hypothesis resulted also from the large quantities, and was supported by a positive correlation between drift and production rate (Waters and Hokenstom 1980).

Unfortunately, after all this work and in spite of how interesting it has been, we are not very well along toward an understanding of the role of drift in the dynamics of the stream ecosystem. In a recent paper, Bogatov (1988) suggested research with the converse approach — that is, to view drift as a factor affecting the rest of the stream community, particularly secondary production. Another gap in our knowledge is how drift may merge with the stream continuum concept; virtually nothing is known of longitudinal variation in drift nor how it may coordinate with the way other stream communities vary along the continuum.

5. Primary production. The estimation of primary production, or photosynthesis by aquatic plants, in the stream channel is an area in which, unfortunately, we have not made good progress. The 1950's witnessed a spurt of research on stream primary production, stimulated apparently by new technologies such as oxygen metering, chlorophyll-measuring spectrophotometry, carbon-14 methodology, and others (Odum 1956; McConnell and Sigler 1959). In special applications, such as open streams with abundant macrophytes (Edwards and Owens 1962) and desert streams (Busch and Fisher 1981), photosynthesis estimates have appeared high enough to supply a stream's energy requirements at the primary level. But estimates in wooded streams suggested that autochthonous primary production might not be sufficient to support the rest of the stream community, and before this apparent paradox was fully investigated, the understanding of allochthony at the primary level made great progress. Thus we soon came to know how food and energy was being supplied to the secondary producers from outside the stream channel, and, in a sense, the solution was discovered before the problem was fully realized.

The Allen Paradox

An analogous paradox has existed for a long time between the next two higher trophic levels, i.e., in the relationship between benthos and fish production. The problem stems from Allen's (1951) classic studies of the brown trout in the Horokiwi Stream, New Zealand. He reported very high levels of annual production by the brown trout, but benthos stocks far too low to support the calculated trout production. It was labeled the "Allen Paradox" by Hynes (1970). The discrepancy has been observed in many subsequent studies (see review by Waters 1988).

Toward a resolution of Allen's results from the Horokiwi Stream, some possible corrections have been suggested (Gerking 1962; Chapman 1967; Le Cren 1969), but even with corrections, the discrepancy remains large. The Allen Paradox has continued to be of critical concern (Allan 1983; Benke 1984; Berg and Hellenthal 1991), but no full resolution has been reached.

The difficulty of stream benthos sampling is well known, and many, if not most, estimates of benthos standing stocks have probably been underestimates (e.g., Kroger 1972). Greater care and thoroughness in bottom sampling are obvious first choices to consider (Allan 1983; Berg and Hellenthal 1991), but totally accurate estimates of the traditional benthos (i.e., in-channel, superficial substrate sampling) probably will not entirely resolve the paradox.

Several sources of trout foods other than the traditional benthos were suggested in a previous review (Waters 1988). These comprise sources of invertebrate animals not routinely estimated, although scattered reports have been published that indicate their importance.

These and other suggested sources of fish food include: (1) the hyporheos, the assemblage of aquatic invertebrates occurring deep within the gravel of the stream substratum (Coleman and Hynes 1970; Allan 1983; Williams 1984; Smock et al. 1992); (2) the snag habitat, submerged brush and other woody debris, providing a stable substrate for filter-feeders such as black fly and hydropsychid larvae (Benke et al. 1985); (3) floodplain production, the development of sometimes large populations of aquatic invertebrates in seasonally inundated floodplains, organisms which may subsequently disperse to the stream (Gibbs and Mingo 1986; Smock et al. 1992); (4) terrestrial invertebrates, insects such as Coleoptera, Lepidoptera, Hymenoptera, and Homoptera, as well as spiders and terrestrial oligochaetes (Hunt 1975; Zadorina 1989); (5) the meiofauna, largely small chironomids and oligochaetes, which occupy fine sediments on stream bottoms, often in high densities, and which are particularly important as first foods of larval fishes (Benke et al. 1984; Soluk 1985; Berg and Hellenthal 1991); (6) benthic microcrustaceans, such as harpacticoid copepods and ostracods, occurring even in small, swift streams sometimes in large quantities (O'Doherty 1985; Shiozawa 1986; Kowarc 1990); (7) small fishes, particularly sculpins occurring with trout in small streams, sometimes in large populations exceeding that of the trout (Mann 1971; Krueger and Waters 1983; Williams and Harcup 1986); (8) cannibalism, possibly to a large degree, is another possibility.

Other possible sources of fish food include zooplankton, small insects, and fish originating from upstream lakes and reservoirs (Lillehammer 1973; Gibson and Galbraith 1975; Peterson et al. 1987); drifting invertebrates from an upstream, predominantly riffle system with high benthos production but few fish, to downstream reaches highly productive of fish (Needham 1928); consumption of eggs, often in large quantities, from anadromous fishes, e.g., smelt eggs (Thonney and Gibson 1989), or from large spawning salmonids.

Few of these alternative fish-food resources have received attention in past benthic studies. Most works on one or several of these possibilities have been in isolation from others. Needed now, to resolve the paradox, are thorough studies of all possible alternatives, concomitantly with fish production estimates.

Allochthony at the Secondary Producer Level

The appreciation of allochthony at the primary producer level has been one of the major progressions in the dynamics of stream ecological theory. The input of plant matter of allochthonous origin contributes energy, nutrients, and substrates in a variety of important ways. That appreciation — leading to the functional group analysis of the macroinvertebrate community and the River Continuum Concept — forced the holistic view of the stream catchment, and it changed drastically our perspective of streams.

The rate of allochthonous input — or rather the proportion of primary productivity of allochthonous origin — varies greatly. In some reaches of streams autochthonous primary production is nearly the total source of energy (Minshall 1978). The proportion of allochthonous input varies over a gradient, ranging from near zero in Deep Creek, Idaho (Minshall 1978) to near 100% in Bear Brook, New Hampshire (Fisher and Likens 1973), and the totally autochthonous stream can simply be viewed as the zero point on the gradient.

At whatever point on the gradient a given stream may lie, it seems certain that the combination of autochthonous and allochthonous primary materials would be sufficient to support the rest of the stream's biological community.

To complete the full appreciation of allochthony, however, it now seems essential to consider the input of materials at higher trophic levels. A full recognition of the holistic view demands that consideration of the allochthonous influence be extended to all higher trophic levels.

A major error in fish trophic ecology may be that we have relied almost totally upon the view that that relationship is simply between fish and benthos. That is, we have long considered the superficial benthos — mainly aquatic insects inhabiting the surface substratum of gravel and stones on the bed of the stream channel — as the principal, or even the sole, food resource for fish. It seems probable now that it was this narrow view of the fish-food resource that has delayed resolution of the Allen Paradox.

All of the suggested additional resources listed in the previous section — the hyporheos, snag habitat, floodplain production, terrestrial invertebrates, the meiofauna, benthic microcrustaceans, small fishes, drift from upstream reservoirs or riffle systems — all may be considered as allochthonous from the viewpoint of the traditional benthos. The trophic ecology of stream fishes now obviously must be concerned with more than the traditional superficial benthos. The Surber sampler, as valuable as traditionally it has been, can no longer be employed as the sole piece of equipment by the fisheries biologist desiring to measure the productivity of a stream's fish-food resource.

And yet a still broader view is needed. We need not only to consider, measure, and integrate fish-food resources, other than the benthos into the trophic ecology of fish, but we need also to integrate all such allochthonous inputs along the stream continuum. In particular, we need to interject fish productivity in the broad sense into the continuum. The holistic view expanded our scale from the stream channel to the catchment, and the river continuum concept expanded our scale of observation from the study reach to the entire profile. But so far this theory development has included only allochthonous input of primary, or plant, materials. The expansion of scales is critically significant, and it would seem especially important in energy dynamics at all levels of community organization.

We should know the downstream distribution of benthos production and its utilization by fish. But in addition to the benthos production, we also need to know the rate of input (or "productivity") of allochthonous animals — hyporheic, terrestrial, etc., along the continuum. Invertebrate drift along the profile, its kinds, its causes, and its utilization by fish, are all important to gaining more complete insight into the basis of fish production. The major missing link appears to be secondary production along the continuum in relation to primary production (autochthonous and allochthonous) upon which the secondary producers depend, as well as how these mainly invertebrate animals affect, and are affected by, fish productivity.

Atlantic Salmon and Stream Dynamics

A large literature exists on the biology and population dynamics of juvenile Atlantic salmon in streams, leading to smolt production (e.g., book of Mills 1989).

Only a few estimates of biological production by juveniles have been published (review by Gibson and Myers 1986). Chadwick and Green (1985) estimated production in a Newfoundland watershed where the major portion of production was in lakes, and Gibson and Haedrich (1988) reported high densities and growth rates (indicating high production) in a Newfoundland city stream enriched with domestic effluents. A few estimates have been published from European streams (Mann 1971; Power 1973; Bergheim and Hesthagen 1990), but a broad-based dataset on biological production of juvenile Atlantic salmon in streams remains yet to be acquired.

In view of the general occurrence of soft, or low-alkalinity, waters in the igneous-based streams of eastern Canada and northeastern United States (Farmer et al. 1981; Haines 1981), production of Atlantic salmon juveniles in North American streams might be expected to be at relatively low levels, probably less than 50 kg · ha^{-1} · yr^{-1} (review of Waters 1977). Data from the Restigouche and Miramichi river systems in New Brunswick ranged from about 3 to 50 kg · ha^{-1} · yr^{-1} (Randall and Paim 1982; Randall and Chadwick 1986).

Feeding behavior of Atlantic salmon parr, as summarized by Mills (1989), includes a predominance of feeding on drift as opposed to bottom foraging. Parr also established feeding territories or stations. They appear to feed less on surface terrestrials than do other stream salmonids, but salmon parr exhibit a relative shift to surface feeding with increasing size and age. The separation in feeding niches between sympatric and possibly competing species such as brown trout or brook trout (*Salvelinus fontinalis*) thus apparently allows greater use of food resources (also reported by Gibson and Cunjak 1986). Thonney and Gibson (1989) and Williams (1981) also reported less feeding on terrestrials by salmon than by brook trout and greater feeding on terrestrials by larger parr than by smaller ones. Therefore less competition appears between brook trout and small salmon, than between brook trout and larger salmon parr.

Very little is known about the basic productivity of salmon streams or the production of the invertebrates. In Mills's (1989) book, which is the current definitive treatise on the ecology of Atlantic salmon, he quotes feeding behavior but no data on stream benthos. Most reports available list the taxa of invertebrates present in the streambed (Peterson et al. 1987) or in the drift (Grant 1967; Peterson and Martin-Robichaud 1986), and the Atlantic salmon feeding relationship to the taxa present (Allen 1940; Keenleyside 1967; Williams 1981), but few quantitative data except for density. Exceptions containing data on biomass include Gibson and Galbraith (1975) in the Matamek River, Quebec, and Gibson et al. (1987), who studied benthic invertebrates with artificial substrates (basket samplers) in several Newfoundland rivers. Williams and Hynes (1974) presented some data on the hyporheos in the Matamek River.

No estimates of benthic production, or of other fish-food resources, apparently have been made or published for North American Atlantic salmon streams.

The exceptionally high densities and growth rates of Atlantic salmon juveniles in city waters receiving domestic effluents, with consequently high levels of phosphorus and nitrogen, suggested potential management strategies for increasing production (Gibson and Haedrich 1988). The fish response, presumably, was due to an increase in invertebrate foods, but no data on this important element were included. The authors called for intensified research into experimental fertilization and the link between fish food and survival and growth.

Clearly, there exists a gap in our knowledge of the ecology of Atlantic salmon in North American rivers. Knowledge of productivity of the benthos, drift, terrestrial inputs, and possibly other allochthonous inputs, their dependence upon autochthonous and allochthonous primary materials, and their utilization by juvenile salmon, would seem to hold great potential for increased management capability for this highly valued fishery resource.

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Limits to Productivity in Streams: Evidence from Studies of Macroinvertebrates

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The density and growth rates of lotic salmonids are in general a positive function of available prey biomass, although other factors may also limit population size. Field data suggest that biomass of macroinvertebrate populations is positively correlated with their food supply. Thus it has been hypothesized that many populations of benthic macroinvertebrates in streams may be limited, or regulated, by food. Correlative studies as well as manipulations of macroinvertebrate densities and food supply for a diverse array of trophic categories and species support the food limitation hypothesis; this appears to be a common constraint on the productivity of stream communities. Current models of stream ecosystem function neglect the nature of the feedback loops which regulate system structure. Evidence from a series of studies summarized here suggests that certain interactions, such as algal–grazer interactions, are strongly coupled while other interactions are less tightly linked. Moreover, these observations suggest a system in which a trophic cascade from salmonids down to benthic productivity is highly unlikely, and macroinvertebrate mortality losses to fish predation are compensatory. While data to determine the strength of coupling between trophic levels, and whether the salmonid–benthos interaction is donor controlled are lacking, the evidence supports the hypothesis that benthic production limits salmonid production.

La densité et le taux de croissance des salmonidés lotiques sont en général reliés positivement à la biomasse disponible pour la prédation, mais d'autres facteurs peuvent aussi limiter la taille de la population. Les données recueillies sur le terrain semblent indiquer que la biomasse des populations de macroinvertébrés est positivement corrélée à leur approvisionnement en nourriture. On a donc posé l'hypothèse que de nombreuses populations de macroinvertébrés benthiques des cours d'eau peuvent être limitées ou régulées par la nourriture. Des travaux de corrélation ainsi que des manipulations des densités des macroinvertébrés et de l'approvisionnement en nourriture pour une série diverse de catégories trophiques et d'espèces viennent étayer l'hypothèse de la limitation par la nourriture; cela semble une contrainte courante de la productivité des communautés lotiques. Les modèle actuels de la fonction de l'écosystème lotique négligent la nature des boucles de rétroaction qui régulent la structure du système. Les indications fournies par la série d'études résumées ici montrent que certaines interactions, notamment celles des brouteurs d'algues, semblent fortement couplées, tandis que d'autres sont moins étroitement liées. En outre, ces observations semblent révéler un système dans lequel une cascade trophique descendant des salmonidés à la productivité benthique serait très peu vraisemblable, et où les pertes par mortalité des invertébrés due à la prédation par les poissons jouent un rôle compensatoire. Si nous manquons de données pour déterminer la force du couplage entre les niveaux trophiques, et pour savoir si l'interaction salmonidés–benthos est contrôlée les don neurs, les indicateurs semblent étayer l'hypothèse selon laquelle la production benthique limiterait la production de salmonidés.

Introduction

The issue of what determines the limits of productivity in aquatic systems has been primarily motivated by interest in commercial and sports fisheries. An intrinsic interest also exists from an ecological viewpoint. Huntsman (1948) was among the first to suggest that moderate cultural enrichment of streams might lead to increased productivity. Many others have made similar observations since (Ellis and Gowing 1957; Hynes 1969). The obvious underlying hypothesis is that productivity of benthic populations is constrained by nutrients and that fish production will in turn be limited by benthos. However, increased productivity at particular trophic levels, or for a particular taxon, may not result in increased productivity at higher trophic levels for many reasons, e.g., non-consumptive losses to hydrologic disturbance, or other energy sinks such as predaceous species other than salmonids. Thus production at lower trophic levels may only set a potential upper limit on productivity.

Considerable evidence shows that growth rates and density of lotic salmonids are positively related to aspects of the prey supply (Chapman 1966). The interaction between food supply and density of salmonids is complicated (Chapman and Bjornn 1969), but density (or biomass) and growth rates are in general higher where prey availability is higher. Salmonid standing stocks are often positively correlated with biomass of benthic prey (e.g., Murphy et al. 1981). Data on productivities are rarer than biomass data, but the two measures should be positively related unless growth rates decrease with increased density, which occasionally occurs. Experiments providing supplemental food directly to salmonids have demonstrated that density and individual growth are sometimes food limited (Mason 1976). Thus it is critical to understand the processes which constrain production of the benthic prey base and the nature of interactions among trophic levels which could affect prey supply to salmonids.

Perspectives are varied on the regulation of populations in streams, as well there is the view that lotic populations are totally unregulated and instead are limited by disturbance, such as flooding. The perception that abiotic effects overwhelm the role of species interactions is being replaced by the awareness that even at low densities certain interactions may have large effects on community structure (Power et al. 1988) and there is likely to be a strong interaction among abiotic and biotic factors (McAuliffe 1984a). Given that many stream invertebrates have tremendous biotic potential by virtue of high rates of reproduction and short generation time, there are orders of magnitude of scope for increase in biomass of populations annually. Added to this, the many taxa at each trophic level usually have differences in phenology such that there are long periods of recruitment and a strong probability that productivity of a trophic level may track productivity in its food supply. This provides the basis of the hypothesis that productivity within any given trophic level may be regulated, or at least limited, by food supply.

The rate of production of benthos will set an upper theoretical limit to the rate of salmonid production (Fig. 1). This hypothesis is simply a thermodynamic rule for the transfer of energy between trophic levels for those fish feeding primarily on macroinvertebrates. At higher rates of benthic production or higher densities, other factors are likely to limit fish populations, such as the availability of suitable instream cover, spawning area, or density-dependent predation upon fish. Many other aspects of the fish-benthos trophic interaction may result in empirically measured production estimates different from any theoretical relationship. Nevertheless, given that prey availability may set an upper bound to fish production, we can profitably ask what determines the productivity of the benthos.

In this paper I will focus on some of the evidence demonstrating that benthic populations can be food limited (by food quantity, quality, or both). The studies which test the food-limitation hypothesis can be grouped into three categories, (i) simple correlations between food supply and population size, (ii) evidence for food-mediated density dependence through manipulations of density, and (iii) experimental manipulations of food supply. In the second part of this paper I discuss a systems approach to a model of trophic interactions in streams. In particular I focus on some of the unstated or untested assumptions commonly used in stream ecosystem theory and point out the importance of the feedback loops between levels as critical research questions. In many instances I have generalized and simplified complex interactions to make a point; real communities are not as simple as a trophic-level model might suggest. This review is not exhaustive, but is intended to illustrate the kind of patterns which are being uncovered and to point out some of the implications of these patterns for the productivity of stream salmonids.

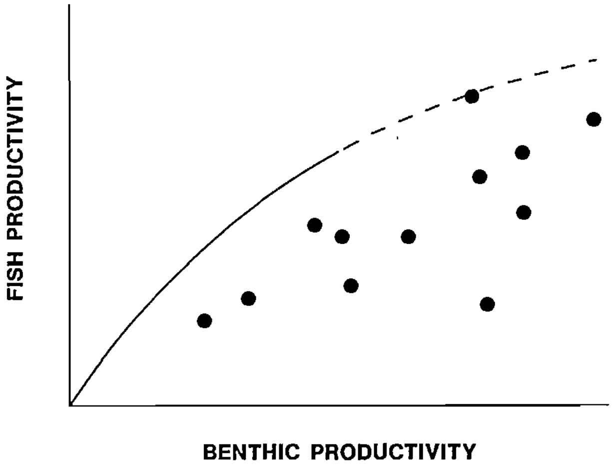

FIG. 1. Theoretical relationship between production of benthos and fish production. The line indicates the potential maximum transfer of energy from benthos to fish. The line is asymptotic since at higher benthic productivities other factors such as suitable habitat or intraspecific aggression may limit fish production. Empirical measures of the relationship may fall below the theoretical maximum, as suggested by the solid circles (not based on real data), since there are other sinks for energy transfer and non-consumptive losses of benthic production. Type of stream bottom may also affect the proportion of benthic production available to fish.

Evidence of Limits to Benthic Productivity

Correlative Evidence

Positive correlations between food abundance and benthic consumer density are a common result of comparisons between streams or between patches within a stream. These relationships may be interpreted as evidence that food density sets limits to consumer populations and that these organisms respond to food distribution; however, alternative interpretations are many. In particular the connection between biomass and productivity is unclear, but across stream systems is likely to be positively related. In this section I give some representative examples of the correlations between biomass at adjacent trophic levels, rather than present an exhaustive review.

Many studies have found positive associations among densities of shredders, or of all macroinvertebrates combined, and the abundance of detritus in benthic samples within a stream. Egglishaw (1964) was the first to show this relationship with detritus for all macroinvertebrates combined and other authors have also shown similar patterns (Mackay and Kalff 1969; Drake 1984). More specific relationships between the density of shredders and the standing stock of coarse particulate organic matter (CPOM) are also widely reported (Hawkins and Sedell 1981; Flecker 1984).

A widely observed pattern of high densities of filter feeders in lake outflow streams is generally correlated with the abundance, quality, or both, of suspended particles in water leaving lakes (Richardson and Mackay 1991). The densities of such consumers decline according to a negative exponential model with increasing distance from the lake outlet (Sheldon and Oswood 1977). The pattern is usually attributed to food supply but other factors, such as the physical and chemical environment, cannot be ruled out based on currently available data (Richardson and Mackay 1991).

Both grazers and predaceous invertebrates tend to show a positive relationship between their density and that of their resources. Hawkins and Sedell (1981) found a weak correlation between grazer density and standing stock of algae measured as chlorophyll *a* across four Oregon streams. There is much more experimental than correlative evidence for the grazer–algae interaction in streams. The role of predaceous invertebrates as energy sinks, or their potential role in the population dynamics of their prey, are not at all well known in spite of considerable interest in the behavioural interactions between these organisms.

Evidence of Food-Mediated Density Dependence

A number of experimental field manipulations have demonstrated intraspecific, density-dependent reductions in growth rate or survival with increased consumer densities. Most of these studies have involved grazer–periphyton interactions. Field manipulations of grazers have shown depression of periphyton standing crops with experimentally increased consumer density (McAuliffe 1984b; Hart 1987; Lamberti et al. 1987). A result found in most studies is a density-dependent decrease in consumer growth rate, observed in grazers such as the caddisflies *Helicopsyche borealis* (Lamberti et al. 1987) and *Glossosoma nigrior* (Hart 1987), and the mayfly *Ameletus* (Hill and Knight 1987). In a manipulation of the density of a shredder *Lepidostoma roafi* (Trichoptera), there was a reduction of growth rate at higher larval densities (Richardson, unpublished data). In some of these studies there was also a density-dependent decrease in survival (Lamberti et al. 1987; Richardson — unpublished data), but in other cases survival rate did not change with density (Hart 1987; Hill and Knight 1987).

Interspecific competition may also be food-mediated through exploitation. McAuliffe (1984b) was able to show that the density of other grazers varied inversely with the density of *Glossosoma* larvae. The mechanism was apparently exploitative competition for algae. The grazing caddisfly *Leucotrichia pictipes* has been shown to exclude conspecifics and other grazers from a territory around its fixed retreat and the area defended is inversely proportional to the density of algae (McAuliffe 1984a; Hart 1985).

The results of these kinds of experiments demonstrate that food resources can be depressed and that the ambient densities of benthos are often set by available resources. These kinds of experiments also reveal the sorts of feedback mechanisms that can lead to regulation of benthic populations and trophic levels.

Experimental Food Supplementation

A number of whole-stream fertilization studies have suggested limitation of benthic production. The earliest of these involved adding bags of inorganic fertilizers to a stream in Nova Scotia. In contrast to an unfertilized stream, algal production, grazer density, and fish size apparently increased (Huntsman 1948). Sucrose used to enrich sections of an Oregon stream increased bacterial biomass, increased standing crops of benthic macroinvertebrates, and reduced per capita drift rates of macroinvertebrates. The result of these changes in the benthos translated to increases in growth of stocked cutthroat trout (*Oncorhynchus clarki*) in three different years (Warren et al. 1964). Addition of inorganic phosphorus to a stream in Alaska increased primary productivity and resulted in increases in growth of some species of benthos, e.g., larval black flies and larval midges of the genus *Orthocladius* (Peterson et al. 1985). A whole-stream fertilization trial on Vancouver Island, Canada, resulted in large increases in periphyton production (Perrin et al. 1987) and in growth and survival of fish, but surprisingly no effect on macroinvertebrate numbers was measureable (Johnston et al. 1990).

Mesocosm studies of the addition of organic materials to flow-through troughs have led to increases in macroinvertebrate densities in a series of experiments by Mundie and co-workers (Mundie et al. 1973, 1983; Williams et al. 1977), presumably by aggregation or enhanced survival. The particular kinds of organic materials added (grains, soybean, fish pellets, fish faeces) were chosen to be inexpensive and readily available. In these experiments most of the increased biomass of benthos was due to colonization by chironomids and oligochaetes. These experiments showed that the densities of some benthos were limited by food.

Population limitation by food may be seasonal and may create periods of resource shortage which can constrain population density of benthic macroinvertebrates. While coarse detritus is abundant at some times of year, low standing stocks during summer create bottlenecks for survival and growth of consumers that limit productivity. In a set of experimental streams I manipulated the input rate of whole-leaf detritus during summer to test the food limitation hypothesis (Richardson 1991). Addition of extra food resulted in large increases in densities of a number of shredder taxa through increased colonization and survival. Increases in growth rates due to food addition were obvious from the differences in adult mass at emergence. The supplementation of leaf litter also resulted in significant reductions in per capita drift rates. Even those taxa which grow primarily during autumn showed retarded growth and lower densities from food limitation early in their life cycle at natural input rates of detritus (Richardson 1991).

Transplants of a lake-outlet filter-feeding caddisfly showed that quality of food was responsible for large differences in growth rates (Richardson 1984). This same filter feeder has been shown to grow faster on high quality laboratory diets than using field-collected seston (Richardson 1984). Additions of coarse detritus to experimental stream channels resulted in significant increases in the density of filter feeders, presumably as a response to increased concentrations of fine organic particles produced by shredders (Richardson and Neill 1991).

Grazers appear to be the trophic group most obviously resource limited from the small-scale density manipulations discussed earlier. In a simple experiment with flow-through troughs using phosphorus amendment, Hart and Robinson (1990) showed increased periphyton growth which resulted in reduced territory size and increased densities of two sessile species in contrast to control troughs. Kohler (1985) showed that in the laboratory *Baetis* exhibited reduced patch residence time and higher drift rates when algae on tiles was experimentally reduced. Mundie et al. (1991) showed that addition of inorganic phosphorus to flow-through troughs increased algal accrual rates, densities of macroinvertebrates, and numbers of emerging aquatic insects in accordance with the food limitation hypothesis.

All of these studies suggest that population limitation, and perhaps regulation (sensu Sinclair 1989), mediated through food supply occurs in stream invertebrate communities. What is not clear is whether food limitation is always the case or under what conditions or during which season(s) these results hold. No long term (> 1 year), controlled, replicated tests of limits to productivity in streams have been conducted. While the increases in biomass observed after food supplementation may be transient, there seems to be little doubt that productivity is constrained by the supply of food or nutrients. Available data suggest that the observation is general and most trophic levels are affected.

Models of Lotic Communities

During the past two decades, models of stream ecosystems have been developed and form much of the basis for current research (Cummins 1974; Vannote et al. 1980; Minshall 1988). These models are basically in the form of "who eats what" and caricature the flow of energy and materials through various ecosystem components. Critical elements missing from these models are the feedback mechanisms which regulate population and trophic interactions. Feedback loops may be a result of resource-mediated exploitative competition that results in density dependence, or non-trophic-resource interactions providing within trophic level or within population feedback (Fig. 2). Generalized systems models based on trophic levels have recently been the focus of much limnetic research using such terms as cascading trophic interactions, bottom-up-top-down regulation, and complex interactions (Carpenter et al. 1985; McQueen et al. 1986; Carpenter 1988). To date most lotic research concerned with regulatory processes have been studies of specific interactions (e.g., Newbold et al. 1983; Power et al. 1985; Hart 1987; Power 1990; Richardson 1991). One study which considered a full trophic level approach is that of Bowlby and Roff (1986) based on a descriptive survey in which they contrasted trophic models based on different types of limits on productivity.

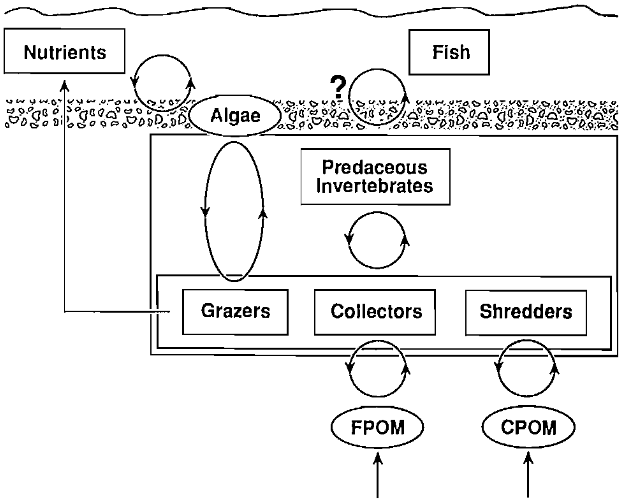

Fig. 2. Outline of a simplified, trophic-level model of stream communities with an emphasis on the major feedback loops which regulate system structure. Each component may be self-limiting for reasons other than exploitative competition for resources and feedback loops within each element could be further added to the ecosystem outline illustrated here. There are many other potentially important direct and indirect effects that may link components of the lotic community which have not been included. The benthic community is shown as a singular entity since the relationship between benthos and fish is unknown in a population or trophic dynamics sense. Shredders are consumers of CPOM such as leaf litter, and collectors are consumers of fine particulate detritus obtained by filter feeding or active collection. CPOM = coarse particulate organic matter, and FPOM = fine particulate organic matter.

One question at the heart of understanding how lotic systems function is to identify which feedback loops are strongly regulating in stream ecosystems. Only those interactions that are strongly coupled (i.e., rapid and strong feedback) are likely to be stable and lead to regulation. The apparent link between algae and their nutrients is tightly coupled. Algae show strong evidence of nutrient limitation and rapid response to nutrient amendment in many cases (Grimm and Fisher 1986; Perrin et al. 1987; Pringle 1987). The coupling between grazers and algae has also been shown to be significant, as discussed above. Other data suggest that grazers may affect periphyton productivity through consumption which increases nutrient renewal rate and reduces shading within the periphyton (McCormick and Stevenson 1991). Interactions other than nutrients-algae-grazers may be tightly coupled, for instance bass preying upon minnows in prairie streams (Power et al. 1985). The stability of any ecosystem is determined by regulatory processes acting within it. Until recently these processes have been neglected in previous ecosystem models of streams. One component of stream communities which is not regulated within the system is the input of detritus, which is an external input to streams, i.e., they are open systems. Models for some closed systems have suggested that detrital pathways add to structural stability of communities (DeAngelis et al. 1989). This stabilizing effect is primarily through detritus acting as a buffer to variation in primary productivity. Because the supply of detritus is donor-controlled, i.e., the renewal rate of detritus standing stock is not determined by consumption by consumers, renewal rate of detritus cannot be depressed in the same way that productivity of algae or prey species can be by overexploitation. This hypothesis also suggests that detritivore population dynamics may be stabilized in part by the donor-control nature of their food supply. It has been suggested that detritivores as a trophic level are always food limited since detritus does not accumulate indefinitely (Hairston et al. 1960), and there is evidence that lotic detritivores are seasonally limited by food supply (Richardson 1991).

Interactions among species and among trophic levels are complex and lead to an array of system responses to changes in one component. For instance, predatory invertebrates may have a competitive effect on fish or facilitate delivery of prey to fish by altering the behaviour of benthic prey (Soluk and Collins 1988). From the perspective of energy transfer to salmonids, predatory invertebrates might be an energetic sink (if these invertebrate predators are not eaten by fish) or increase transfer rates. These potentially non-linear interactions make stream systems more complicated than the sum of their parts, i.e., understanding pairwise interactions will not lead to good predictive power at higher levels of trophic organization.

The interactions between stream fishes and benthos appear to be primarily unidirectional, i.e., donor-controlled. Some attempts to look at effects of salmonids on stream benthos have shown no significant changes (Allan 1982; Culp 1986; Reice and Edwards 1986). However, other instances of experimental manipulations of stream fish have shown large effects on benthos, but these may have been special cases where refuge within the substrate was limited (Hemphill and Cooper 1984; Power 1990), or prey were algae-eating fish (Power et al. 1985). Population effects of fish-benthos interactions are still controversial and in need of larger-scale experiments.

Discussion

Evidence supports the hypothesis that productivities of lotic macroinvertebrate populations are food limited at a variety of trophic levels. Consistent patterns from studies of resource limitation of lotic macroinvertebrates are the density-dependent reductions in growth rates and survival, and alleviation of these effects by food additions. Also, per capita rates of drift (or movement) decrease as food increases. Nevertheless, a number of important questions remain to be addressed. We do not yet have any indication whether the density dependence observed in small-scale experiments is sufficient to regulate populations and therefore one can only conclude that resources are limiting. Are interactions among components of stream communities strongly coupled and which components are these? How widespread are multi-species interactions, for instance, non-additive effects? There is some evidence to suggest that top-down effects of predators on benthic productivity may exist (Bowlby and Roff 1986; Power 1990), but the relative magnitude of this effect and its generality are unknown and warrents further study.

One of the bigger gaps in our knowledge of stream benthos is an understanding of the demography of macroinvertebrates. Data on the differential rates of mortality of individuals drifting versus those remaining in the benthos are lacking. However, in recent years there is indication that those individuals drifting may be smaller, have less-full guts, and be more frequently parasitized than non-drifting individuals. The fate of drifting individuals is of consequence to determining whether these individuals are in excess of carrying capacity (Waters 1972). Many poikilotherms can survive for a relatively long time when starved; however, in natural populations such a situation can result in overexploitation of the resource base and destabilization of the population interaction because of the lag time between changes in resource productivity and consumer demand. If drift is a measure of the proportion of the population that cannot be supported by available food then perhaps predatory losses to foraging drift feeders will be partly or entirely compensatory.

Examples of the density of prey populations in apparent equilibrium with resource supply are many. Because of the large biotic potential of invertebrates it is likely that biomass could track the productivity of their resources during relatively benign periods between disturbances. One of the questions that remains is what prevents invertebrate populations from overexploiting their resources. Growth, recruitment, and colonization can account for the increases in biomass, but it is the processes that reduce numbers that have been little studied. One potential hypothesis is that there is a strong interaction between food shortage and predation mortality. This might come about if hunger results in elevated rates of drift or other behaviours that modify predation risk. An area that is just beginning to be explored is the role of pathogens on mortality rates of benthic macroinvertebrates. Again, one could predict an interaction between food shortage and the influence of pathogen-induced mortality. Such relationships remain fundamental questions to understand the population biology and potential productivity of stream macroinvertebrates.

The proportion of the prey production consumed by foraging fish, such as salmonids, has been termed the ecotrophic constant. The value of this term will depend heavily on the shape of the mortality-age relationship for prey populations. Macroinvertebrates can produce hundreds to thousands of eggs. The scope for increases in biomass of prey populations is therefore dramatic and only a small proportion of the population need survive for replacement. Thus the value of the ecotrophic constant may be very high, but until we understand more of the demography of prey populations its value will remain elusive.

The possibility that the rate of supply of invertebrates to salmonids is determined by the effects of resource limitation at lower trophic levels would indicate that the nature of the macroinvertebrate-to-fish interaction is donor-controlled. Experiments designed to examine fish effects on benthos have produced conflicting results, but some studies suggest that salmonids have no depressing effect on prey populations (Allan 1982; Culp 1986; Reice and Edwards 1986). The result of course depends on the nature of the substrate and the refuge it provides to benthos, among other possibilities. The view that I have expressed here implies that productivity of salmonids is strongly constrained by productivity at lower trophic levels and means "bottom-up" regulation of production. While many other factors may limit or regulate salmonid populations, food will set an upper limit to productivity.

Factors other than food and nutrient supply may also set boundaries on the potential productivity of some systems. Disturbances associated with hydrologic variation may reduce some lotic populations. However, flow variation may have a greater effect on the abundance of periphyton and detritus than directly on densities of consumers. Available habitat may also limit productivity. The extent of riffle area may be related to overall population density (Bowlby and Roff 1986). Nevertheless, food limitation is an important upper bound that can and does constrain the productivity of stream communities.

Many questions remain to be addressed about the nature of the interactions among salmonids and macroinvertebrates. The net effect of the interaction is still unknown, although there is some suggestion that it is unidirectional and compensatory. While there is now considerable evidence that resource limitation is common for stream benthos, we still do not know if such populations are also regulated by resources and how general that might be. All of these considerations will be important to our understanding of the functioning of lotic communities and to determining the limits to salmonid production.

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Diet Variability in Relation to Season and Habitat Utilisation in Brown Trout, *Salmo trutta* L., in a Southern Irish Stream

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Habitat utilisation by salmonids and the identification of the important factors in habitat selection received considerable attention in the past, but little is known of the impact of such utilisation on other aspects of salmonid ecology, particularly diet. Present field study was undertaken to investigate diet variability in different aged brown trout in relation to habitat, site and season.

The study was carried out in five sites in a single stream, sampling taking place seasonally over 2 years in riffle and pool habitats. Habitat utilisation and diet (using non-destructive stomach flushing techniques) were monitored from fish populations in each site and on each sampling occasion. 0+ and 1+ trout showed differential habitat utilisation.

Diet variation with habitat, fish age, season and site was analysed using the TWINSPAN hierarchical classification technique. This analysis produced clearly defined clusters of samples related to season and within summer and autumn related to habitat. There was little differences in diet during winter and spring. Age and sampling year were also influential but site had no significant effect on diet.

Based on knowledge of prey types and availability in the different habitats, the results suggest the adoption of specific foraging tactics involving pool dwelling fish moving out to forage in riffles at certain times of year. The data support the contention that trout have activity-specific habitats, at least for part of the year, with resting refuges in pool habitats and foraging in riffles.

L'utilisation de l'habitat par les salmonidés et l'identification des facteurs importants dans le choix de l'habitat ont reçu une attention considérable dans le passé, mais on connaît mal l'impact de cette utilisation sur d'autres aspects de l'écologie des salmonidés, particulièrement leur alimentation. La présente étude de terrain a été entreprise pour examiner la variabilité de l'alimentation chez des truites brunes d'âges divers par rapport à l'habitat, au site et à la saison.

L'étude a été menée sur cinq sites d'un même cours d'eau, l'échantillonnage étant effectué de façon saisonnière sur deux ans dans des habitats de radier et de fosse. On a surveillé l'utilisation de l'habitat et le régime alimentaire (à l'aide de techniques non destructives d'irrigation de l'estomac) chez les populations de poisson de chaque site et à chaque opération d'échantillonnage. On a observé que les truites d'âge 0+ et 1+ utilisaient l'habitat de façon différente.

La variation du régime alimentaire en fonction de l'habitat, de l'âge des poissons, de la saison et du site a été analysée par la méthode TWINSPAN de classification hiérarchique. Cette analyse a produit des grappes d'échantillons nettement définies, liées à la saison et, en été et en automne, liées à l'habitat. Il y avait peu de différences dans l'alimentation pendant l'hiver et le printemps. L'âge avait aussi son influence, mais le site ou l'année d'échantillonnage n'avait pas d'effet significatif sur le régime alimentaire.

D'après les connaissances sur les types de proies et leur disponibilité dans les différents habitats, les résultats permettent de penser que les poissons adoptent des tactiques spécifiques d'alimentation dans lesquelles les truites vivant dans les fosses se déplacent pour se nourrir dans les radiers à un certain moment de l'année. Les données confirment que les truites occupent des habitats en fonction de leur activité, au moins pendant une partie de l'année, trouvant refuge pour se reposer dans les fosses et se nourrissant dans les radiers.

Introduction

Studies of survival, distribution and population density of salmonids have recently been described as being of limited value unless they are conducted with reference to habitat (Heggenes and Borgstrom 1991). Considerable work has been carried out on the habitat utilisation of salmonids in Europe, Scandinavia, Canada and USA (Jones 1975; Karlstrom 1977; Gibson 1978; Fausch and White 1981; Egglishaw and Shackley 1982; Kennedy and Strange 1982; Cunjak and Green 1983; Hearn and Kynard 1886; Heggenes and Saltveit 1990).

The general patterns of habitat segregation found amongst sympatric salmonids describe the trout as inhabiting pools with salmon more abundant in the shallow riffles. However, microhabitat preferences amongst salmonid species cohorts are known to change over time, with fish moving from shallow to deeper water as they grow older (Jones 1975; Kennedy and Strange 1982; Elliott 1986).

Comparison of utilisation of habitat and other resources of species living allopatrically or sympatrically help to determine and identify the importance of factors that influence fish distribution

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(Olson et al. 1988). Four habitat variables have repeatedly been referred to as of importance in salmonid habitat selection, water velocity, water depth, substrate and riparian cover (Egglishaw and Shackley 1982; Kennedy and Strange 1982). Several factors other than the habitat itself can also influence habitat utilisation of salmonids (Heggenes 1991). For example, season (Karlstrom 1977; Gibson 1978; Rimmer et al. 1983, 1984; Heggenes and Saltveit 1990), social interactions (Fausch 1984; Metcalfe 1986), predation (Huntingford et al. 1988) and intra and inter specific competition for space and/or food (Chapman and Bjornn 1969; Kennedy and Strange 1986; Gatz et al. 1987).

Although habitat utilisation and the factors influencing habitat selection have been subject to considerable research, there has been little work on the effects of such habitat utilisation on other aspects of the ecology of salmonids, particularly diet. Behavioural studies of fish distribution have been carried out to determine position choice by juvenile Atlantic salmon, *Salmo salar* L., in relation to feeding (Wankowski and Thorpe 1979; Stradmeyer and Thorpe 1987). Fausch (1984) has discussed specific growth rates in relation to profitable stream positions. However, scant attention has been given to the diet of stream dwelling salmonids occupying different habitats and it is to this factor that the present study is addressed. Questions raised include whether the diet of salmonids occupying pools differs from that of fish inhabiting riffles and if so, does diet influence the occupation of such habitats or does it simply reflect differential habitat utilisation?

Site Descripition

The study area, Glenfinish River (mean pH 6.9, conductivity 139 $\mu s \cdot cm^{-1}$) is a third order tributary of the Araglin River in the Munster Blackwater system, County Cork, Ireland. Five sites, each approximately 50–70 m long were selected along the study stream. Physical parameters of each site are outlined in Table 1.

The stream has good populations of breeding brown trout, *Salmo trutta* L.. Atlantic salmon in low numbers, European eel, *Anguilla anguilla* (L.) and a few stoneloach, *Noemacheilus barbatulus* (L.), were also present.

TABLE 1. Estimated percentages of physical parameters of sites 1–5.

	Site 1	Site 2	Site 3	Site 4	Site 5
Average width/m	3.2	3.7	3.1	3.0	2.2
% Riffle	85	20	85	55	65
% Pool	15	80	15	45	35
% Riparian cover	20	40	10	80	75
% Sand	15	80	15	30	35
% Stone	80	20	75	65	65
% Boulder	5	0	10	5	0
Distance to next upstream site/km	0.13	0.32	1.76	1.44	

Methods

From June 1989 to May 1991, regular sampling of brown trout was carried out monthly over summer and autumn and bimonthly over winter and spring.

On most occasions stop nets (mesh size <5 mm) were used to enclose the entire site and to partition the stretch into riffle and pool sections (riffle and pool being quantified by water velocity (Ott flow meter) and water depth), such that fish were prevented from moving between habitats during sampling. Fish were captured between approximately 10:00–12:00 AM, using a 400V pulsed D.C. electrofishing apparatus powered by a 12 V battery. The fish were collected by fishing upstream in the enclosed sections, keeping fish separate from each habitat type. The captured fish were held in perforated buckets, situated in a shallow stretch of the stream.

Following collection, several fish at a time were transferred to a bucket of freshwater with 3-4 drops of quinaldine (2-methyl-quinoline) added as an anaesthetic. The fish were then stomach flushed using a modified version of the Seaburg (1957) technique (Twomey and Giller 1990). The stomach contents were back flushed out of the fishes mouth and collected via a funnel into numbered plastic bottles. Seventy percent ethanol was added as a preservative. The fish were then weighed, using a Pesola spring balance (to the nearest gram) and fork length measured (to the nearest millimetre). Scales were removed from above the lateral line, behind the dorsal fin from representative sized fish. The fish were then transferred to a recovery bucket of freshwater and later returned to the centre of each site. This technique has been shown to have no detrimental effects on fish condition or diet (Twomey and Giller 1990).

Gut contents were examined in the laboratory under a binocular microscope. Prey species were identified to varying taxonomic levels depending on the taxa in question (see Table 3). Age of fish was determined by a combination of scale reading and length-frequency distributions.

The sampling programme provided data over 2 years on (a) habitat preference of different age classes of brown trout from five sites and four seasons within the same stream and (b) diet variation over seasons, site, habitat and age class.

Data Analysis

Habitat utilisation of each age class over 2 years was analysed by two way Analysis of Variance, using habitat and season as the variables. Relative abundance data were transformed using arcsin square root of p_i, where p_i is the proportion of total individuals in each habitat.

Gut contents of fish of similar age and from the same habitat, site and sampling occasion were pooled and converted into percentage composition data, using the number method (Hynes 1950). Variation in percentage composition of invertebrate species in trout stomach contents was examined using a hierarchical classification technique, TWINSPAN (two way indicator species analysis) (Hill 1979). In this technique, the data are first ordinated by reciprocal averaging and those species (in this case dietary components) that characterise the reciprocal averaging extremes are emphasised in order to polarise the samples, and the samples are divided into clusters by breaking the ordination axis near the middle (Gauch 1982). The division process is repeated on the two sample subsets to give four clusters, and so on for a specified number of division levels. This programme classified fish stomach contents within a particular year, season, habitat, site and age group into a diverse hierarchy of clusters of similar invertebrate composition and identified indicator prey species for each dichotomy (i.e. the major prey type and percent value used at that level in the classification to separate the two groups of samples at the dichotomy of the cluster matrix). The TWINSPAN procedure was terminated at level 6.

Results

Occurrence of 0+, 1+ and 2+ brown trout from all sites was significantly different in the two habitats, throughout most seasons and in both years. As expected, younger trout were predominantly found in riffle stretches (*P*=0.01, *P*=0.000, year 1 and 2, respectively), with older trout more commonly found in deeper, slower flowing water (1+ *P*=0.002, *P*=0.001 year 1 and 2, respectively, 2+ *P*=0.000 year 1, Table 2).

TABLE 2. Distribution of 0+, 1+ and 2+ brown trout in riffle and pool habitats at sites 1–5 from (a) 1989–90 and (b) 1990–91.

		Summer		Autumn		Winter		Spring	
		Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool
a) 1989–90									
Site 1	0+	44	14	33	22	28	12	13	3
	1+	23	32	3	26	6	6	53	28
	2+	2	13	0	4	2	4	0	0
Site 2	0+	29	14	21	22	19	18	24	1
	1+	0	48	0	42	2	22	16	44
	2+	0	15	0	16	0	17	0	12
Site 3	0+	51	14	54	24	28	9	2	2
	1+	12	11	7	11	7	0	35	21
	2+	1	4	1	1	4	0	5	2
Site 4	0+	35	22	29	28	3	13	0	16
	1+	10	32	8	28	2	9	51	50
	2+	1	10	0	4	0	0*	5	4
Site 5	0+	27	15	11	41	17	13	0	0
	1+	2	1	0	2	1	0	26	23
	2+	0	2	0	2	0	0	0	0
b) 1990–91									
Site 1	0+	42	6	58	14	14	3	0	0
	1+	31	22	21	31	10	3	22	6
	2+	2	1	0	4	0	0	11	5
Site 2	0+	33	12	40	48	6	21	0	0
	1+	8	50	1	37	2	15	1	20
	2+	0	9	0	4	0	1	0	5
Site 3	0+	30	4	83	20	24	5	4	0
	1+	36	29	13	16	4	6	16	15
	2+	2	1	0	0	1	2	7	2
Site 4	0+	29	11	26	30	21	14	2	0
	1+	25	46	27	23	8	14	21	26
	2+	1	3	0	3	0	2	1	4
Site 5	0+	2	0	0	1	0	0	0	0
	1+	6	24	3	6	6	4	0	0
	2+	0	1	0	0	0	0	0	1*

[a]Summer = June and July, Autumn = August and September, Winter = November and January, Spring = March and May
* Only 1 month of sampling.

The TWINSPAN classification of stomach contents provided a highly significant non-random order of samples (runs test which determines if a given sample has more or fewer runs (succession of identical components) than would probably occur in a random sample (Bishop 1983)), that fell into a series of clusters strongly related to season. An initial dichotomy separated winter and spring from summer and autumn samples. Age, habitat and year of sampling were also influential in organising the sample classification. No association with sampling site was evident from the classification. Whilst a few samples appeared out of position in the classification, 11 main clusters (Groups 1–11) and their indicator species were identified with characteristic season, habitat, age of fish and year of sampling at level 4 of the classification (Fig. 1).

All Groups except 8, 10 and 11 showed little evidence of habitat segregation on fish diet. Group 1 consists of a small group of winter samples of various ages of fish from both sampling years. Group 2 consisted of a small mixture of age classes and seasons (autumn, spring and winter (second year)). Group 3 were mostly larger trout from the second year of spring samples. Group 4 and 5 consisted of fish of all ages feeding in winter of the second and first year, respectively. Groups 6 and 7 were mostly 0+ fish from autumn and summer (year 1), respectively. Group 8 consisted mainly of 0+ and 1+ fish from riffle areas during summer. 1+ and 2+ fish from the first year's spring sampling were classified into Group 9. Groups 10 and 11 included larger fish inhabiting pools in autumn and summer, respectively.

Table 3 describes the dominant prey of each Group 1–11 and the main indicator prey species for the classification are shown in Fig. 1. The main dietary components of the seasonally clustered groups are apparent. The diet of winter feeding fish consisted predominamtly of gammarids, cased caddis, *Philopotamus montanus*, *Plectrocnemia conspersa*, *Hydropsyche* spp., and chironomid pupae. The plecopteran nymphs, *Brachyptera risi*, *Isoperla grammatica* and *Chloroperla torrentium* and ephemeropteran nymphs, *Rhithrogena* and *Ephemerella ignita* were characteristic of the diet of spring feeding fish. Large proportions of chironomid larvae, *Baetis rhodani*, Simuliidae, *E. ignita*, terrestrial and aerial items and adult *Helophorus brevipalpis* (terrestrial beetle, likely to be of drifting origin) were consumed by summer feeding fish. A high consumption of *Dixa* spp., chironomid larvae, chironomid pupae, terrestrial and aerial items, *B. rhodani* and Simuliidae were evident in autumn feeding fish.

Characteristic prey of pool occupying 1+ trout were terrestrial and aerial items, weevils and adult *H. brevipalpis* (both likely to be of terrestrial origin). Greater consumption of *B. rhodani*, Simuliidae and *E. ignita* by riffle occupying trout was also evident.

The increased consumption of *E. ignita*, Simuliidae, terrestrial and aerial items, weevils and decreased proportions of gammarids and *Rhithrogena* in the diet were evident from fish in spring of the first year. Similarly, higher proportions of *Rhithrogena, B. risi*, chironomid pupae, weevils, terrestrial and aerial items and lower proportions of gammarids and *C. torrentium* were evident in the diet of fish in winter of the first year.

TABLE 3. Percentage contribution of dominant prey in stomach contents, coded into categories 1–8[a] in TWINSPAN Groups 1–11.

	1	2	3	4	5	6	7	8	9	10	11
G. duebeni	7	4	5	5	4	4	3	3	4	4	3
B. rhodani	4	4	4	4	4	6	5	5	4	3	3
B. muticus	3	3	2	2	2	2	1	2	2	2	1
E. ignita	-	2	2	-	-	3	3	4	5	3	3
Rhithrogena	3	2	5	2	3	1	3	3	4	2	3
P. meyeri	-	2	3	2	2	2	1	1	1	1	1
B. risi	-	1	3	-	2	-	-	-	2	-	-
L. hippopus	2	2	2	2	2	2	1	2	2	2	2
I. grammatica	2	2	3	2	2	2	1	2	3	1	1
C. torrentium	-	1	2	2	-	-	1	1	2	-	-
Rhyacophilidae	-	3	2	2	2	2	3	2	2	3	1
Hydropsychidae	2	4	3	3	3	2	1	1	3	1	2
P. montanus	4	2	1	2	3	1	1	1	2	1	1
P. conspersa	-	2	1	2	2	1	1	1	1	1	1
Cased caddis	5	3	3	5	4	4	2	2	3	3	3
Chironomid L.	3	5	4	4	5	6	8	5	4	6	6
Chironomid P.	2	2	1	2	5	3	1	1	1	3	1
Simuliidae	2	4	3	3	2	5	5	4	5	3	3
Dixa spp.	-	-	1	2	2	3	2	1	1	3	2
A *H. brevipalpis*	-	-	-	2	2	2	3	3	2	2	6
Weevil	-	-	2	-	2	1	1	1	3	2	3
Terrestrial and aerial	4	5	5	5	6	5	4	5	6	7	8

[a] 1=0–0.5%; 2=0.5–1%; 3=1–5%, 4=5–10%; 5=10–20%; 6=20–30%; 7=30–40%; 8=40–50%.

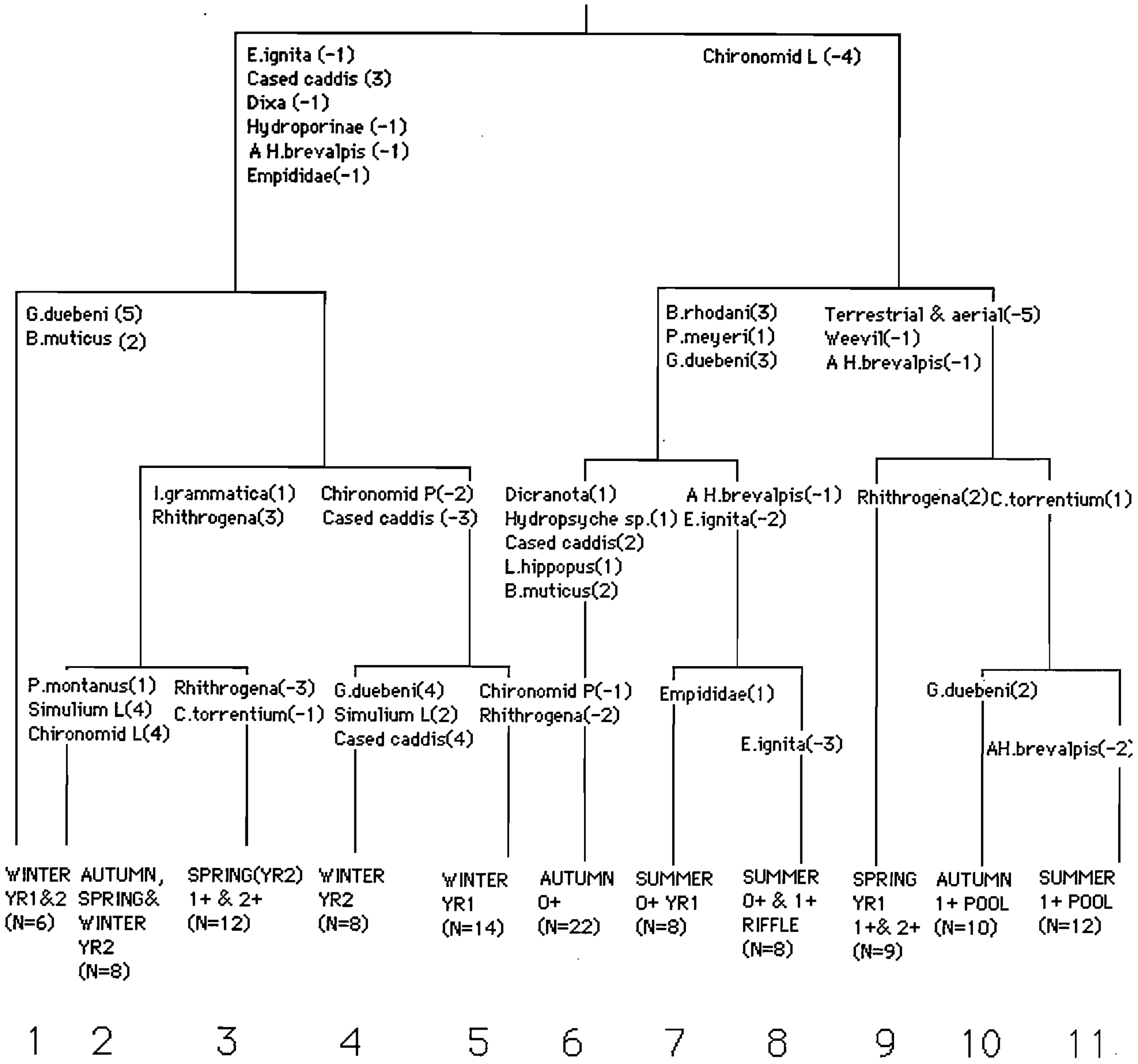

FIG. 1. TWINSPAN hierarchical classification of brown trout stomach contents related to habitat, fish age and season.

Discussion

Microhabitats occupied by 0+, 1+ and 2+ brown trout in Glenfinish River were significantly different. The younger fish tended to occupy riffles and the older trout were more abundant in the pools, in most seasons and at most sites. Similar microdistribution amongst trout cohorts have been observed by Jones (1975), Bohlin (1977) and Kennedy and Strange (1982). The extent to which these differences in distribution were evident was partially dependent on season, as the pattern became less distinct during autumn for 0+ and during spring for 1+ fish, as also discussed by Gibson (1978), Rimmer et al. (1983, 1984) and Heggenes and Saltveit (1990). Habitat availability can also influence habitat utilisation of salmonids (Heggenes 1991). The sites in the present study do differ in habitat availability, with site 2 having least riffle habitat, sites 1 and 3 most riffle and sites 4 and 5 in between (Table 1). Nevertheless, while habitat availability may contribute to differences in habitat utilisation between sites (Table 2, see also Bridcut 1992), site had no significant effect on trout diet as shown by the classification procedure.

In the present study, classification of trout diet was most strongly influenced by season, which accounted for the separation of samples at the early levels of classification. Seasonal variation in salmonid diet has been well documented in relation to availability and consumption of prey organisms (Maitland 1965; Frost and Brown 1967; Mann and Orr 1969; O'Farrell 1983; Kelly-Quinn 1986; Twomey 1988). TWINSPAN classification of Glenfinish benthic communities (Bridcut 1992) shows a very strong seasonal pattern (see also Giller et al. 1990) and such seasonal differences are reflected in the diet of brown trout.

Year of sampling was also seen to influence trout diet. Sampling towards late spring during the first year could have resulted in these spring samples being more closely classified with summer and autumn fish than the early spring samples of the second year. Fish in the first spring consumed a more summer/autumn like diet with higher consumption of *E. ignita*, Simuliidae, terrestrial and aerial items and less gammarids and cased caddis. A less pronounced segregation between sampling years was evident in winter feeding fish, which were sampled at similar times. Benthic communities were classified similarly in both years (Bridcut 1992).

Age was another influential factor in trout diet, as also noted by Frost and Brown (1967), Fahy (1980), Kelly-Quinn (1986) and Twomey (1988). The classification of 1+ spring fish only in Groups 3 and 9 may also be a result of 0+ fish being too small to stomach flush and very few 2+ fish being captured at this time of year.

Age alone, however does not determine the final clustering pattern of trout diet samples. Habitat seems to play an additional role, as all 1+ pool occupying fish are classified in Group 10 and 11 and all 1+ riffle occupying fish are clustered in Group 8. Prey of 1+ pool occupying fish were dominated by terrestrial and aerial items (e.g. adult Diptera, Homoptera, Coleoptera, Hymenoptera, Ephemeroptera, Trichoptera, Plecoptera, Chilopoda, Diplopoda, Lumbricidae and Isopoda), chironomid larvae, adult *H. brevipalpis*, and weevils. The diet of 1+ trout inhabiting riffles was composed largely of chironomid larvae, *B. rhodani*, Simuliidae, terrestrial and aerial items and *E. ignita*. Egglishaw (1967) similarly noted 1+ trout from pools containing more terrestrial organisms and less emerging *Baetis* than 1+ trout from runs. Groups 6 and 7 showed a weaker age related pattern in their diet. Habitat segregation in the diet was not apparent from these mostly 0+ trout, as the diet of both 0+ riffle and pool occupying fish was dominated by chironomid larvae, Simuliidae, *B. rhodani*, terrestrial and aerial items and *E. ignita*.

Salmonids are known to consume both benthic and drifting prey organisms (Kelly-Quinn 1986; Twomey 1988) and these prey sources are therefore discussed by Bridcut (1992) and included in this study.

TWINSPAN classification of Glenfinish benthic riffle and pool communties (Bridcut 1992) described a pronounced habitat segregation of invertebrate communties, particularly in summer and autumn, but winter and spring invertebrate communties were not as clearly partitioned by TWINSPAN classification as for the warmer months (Bridcut 1992).

Drift samples in both riffles and pools were rather similar, consisting of *B. rhodani*, chironomid larvae, terrestrial and aerial items, *B. muticus* and Simuliidae, although pool drift had slightly larger proportions of terrestrial and aerial items and riffle drift had larger quantities of drifting baetids. It is well known that faster water currents carry a larger number of drifting organisms (Everest and Chapman 1972; Wankowski and Thorpe 1979; Fausch 1984; Grant and Noakes 1987).

From the above knowledge of dietary contents of trout over season, habitat and age and of benthic and drifting invertebrates in pool and riffle habitats, it is possible to speculate on the foraging tactics of stream dwelling brown trout in Glenfinish River.

During summer and autumn, 0+ riffle and pool occupying fish have similar diets, that reflects the riffle benthic and drift composition and quantity. This may suggest that 0+ fish inhabiting pools move from the slower habitat to faster water to obtain food. However different foraging tactics are apparent for 1+ trout inhabiting pools and riffles during summer and autumn. This could be a result of different food availability in the two habitats (benthic and drift), or fish from the two habitats may select food of different composition and quantities in the same habitat. The former is more likely, thus 1+ trout inhabiting pools may not move from the slower, deeper habitat to faster, shallower waters, (even though drift quantity will be greater) at that time of year.

Diets of trout during winter and spring showed little evidence of habitat segregation. The benthic invertebrates (Bridcut 1992) were themselves more similar in riffles and pools in these colder months, but also the diet of fish showed a higher consumption of benthic, non-drifting organisms, abundant in the riffle habitats, e.g. gammarids, caddis, with fewer baetids, chironomid larvae and terrestrial and aerial items. This may indicate a movement of the pool fish into faster riffle habitats to feed at this time of year.

Movement from a slower current, lower energy consuming habitat, to faster water, rich in benthic and drifting invertebrates may be energetically advantageous for foraging. Indeed studies have discussed salmonids holding fixed positions, from which they make excursions to intercept drifting invertebrates in nearby fast water (Wankowski and Thorpe 1979; Fausch and White 1981; Fausch 1984; Rimmer et al. 1983;1984; Stradmeyer and Thorpe 1987; Huntingford et al. 1988).

Trout habitat positions observed in Glenfinish River during the day (Table 2) may be those that fish inhabit for resting/refuge purposes. The results of trout diet classification suggest that some fish occupy different foraging positions at certain times of the year. Shirvell and Dungey (1983) have similarly proposed such activity-specific habitats for salmonids.

Trout diets, appear to be partially determined by the habitat in which they forage and therefore we suggest that habitat occupation must be considered in future dietary studies of fish populations.

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Transplantation of Atlantic Salmon (*Salmo salar*) and Crypsis Breakdown

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Crypsis is an important antipredator defense for juvenile salmonids. We tested the hypothesis that transplanted salmonids experience high predation rates due to their poor colour-match to their new surroundings. Atlantic salmon (*Salmo salar*) fry acclimated to brown-coloured laboratory predation arenas without gravel substrate had four times the predation mortality by hooded mergansers (*Lophodytes cucullatus*) as tan-acclimated fish. Tan-acclimated salmon experienced less predation than those acclimated to the brown background regardless of predation arena colour, suggesting that Atlantic salmon may be unable to colour-acclimate to all backgrounds equally well, or that gravel substrates are integral for crypsis of strongly parr-marked fishes. Two rivers in southern Quebec having recently introduced populations of either Atlantic salmon or rainbow trout (*Oncorhynchus mykiss*) were sampled to determine whether colour mismatch to their new habitats persists in years following transplantation. Species which have evolved at a given site were predicted to converge on similar antipredator coloration, while introduced species were predicted to differ in coloration and have greater predation risk than native brook trout (*Salvelinus fontinalis*). Compared to native brook trout, Atlantic salmon introduced to the Satarouski River generally had lighter coloration and nearly three times the frequency of predation scars, while self-introduced rainbow trout in the du Gouffre River were darker and had 1.5 times the frequency of scars. Colour-matching of appropriate stocks to habitats and acclimation of fish to substrates having similar coloration to the substrate where they will ultimately be transplanted may decrease the likelihood of loss of transplants to predators.

L'homochromie constitue pour les salmonidés juvéniles un moyen important de défense contre les prédateurs. Nous avons essayé de démontrer que les salmonidés transplantés connaissent des taux élevés de prédation à cause de leur faible mimétisme dans leur nouvel environnement. Des alevins de saumon atlantique (*Salmo salar*) acclimatés en laboratoire à des arènes de prédation colorées en brun, sans substrat graveleux, ont présenté un taux de mortalité due à la prédation par le bec-scie couronné (*Lophodytes cucullatus*) quatre fois plus élevé que chez les poissons acclimatés à un milieu de couleur ocre. Ces derniers présentaient une prédation moindre que les spécimens acclimatés à un fond brun quelle que soit la couleur de l'arène de prédation, ce qui semble indiquer que le saumon atlantique peut être incapable d'adaptation mimétique égale dans tous les milieux, ou que les substrats graveleux sont indispensables à l'homochromie chez les poissons portant de nettes marques de tacon. Nous avons échantillonné deux rivières du sud du Québec possédant des populations récemment introduites de saumon atlantique ou de truite arc-en-ciel (*Oncorhynchus mykiss*) pour déterminer si le défaut d'homochromie dans le nouvel habitat persiste dans les années qui suivent la transplantation. On prévoyait que les espèces qui avaient évolué à un site donné allaient atteindre une coloration antiprédation similaire, tandis que les espèces introduites pouvaient différer en coloration et courir davantage de risques de prédation que l'omble de fontaine indigène (*Salvelinus fontinalis*). Par rapport à cette dernière espèce, le saumon atlantique introduit dans la rivière Satarouski présentait en général une coloration plus pâle et près de trois fois la fréquence de cicatrices de prédation, tandis que la truite arc-en-ciel auto-introduite dans la rivière du Gouffre était plus sombre et présentait 1,5 fois la fréquence de cicatrices. La recherche d'une homochromie entre les stocks et les habitats et l'acclimatation des poissons à des substrats présentant une coloration similaire à ceux où ils seront transplantés peut faire décroître les possibilités de pertes par prédation.

Introduction

Natural selection regulates the presence and persistence of adaptations promoting survival (Owen 1980). Endler (1986) showed that mortality selection is the most commonly demonstrated component affecting fitness and that morphological traits are more likely to be selected than physiological or biochemical traits. Predation is more commonly demonstrated as a selection mechanism than competition or abiotic factors. While selection usually promotes genetic stability of a population so that trait distributions do not change markedly from generation to generation, if environmental changes occur, or populations are introduced to habitats that differ markedly from the original habitat, frequency distribution changes occur (Endler 1986). An excellent example is predator selection on the peppered moth (*Biston betularia*) in post-industrial Great Britain (Kettlewell 1973). Our study examines predator selection on transplanted salmonid fishes.

Most predators visually searchfor prey and crypsis or camouflage is used extensively by prey to avoid predator detection (Cott 1957; Robinson 1969; Edmunds 1974). The criteria by which presumptive examples of crypsis are evaluated (Suffert 1932, cited in Robinson 1969) are convergence with other species on similar colours, patterns or forms (e.g., leaf and twig mimics), convergence on behaviours expected of cryptic organisms and demonstrations that the characters conceal the organism.

Juvenile salmonids have long been assumed cryptic (Hoar 1958; Nikolsky 1963; Denton 1971; Hawkes 1974; Davies and Thompson 1976; Hasler et al. 1978; Ruggles 1980; Noakes 1980), but testing the hypothesis or understanding management implications has occurred only recently. Donnelly and Dill (1984) predicted that if crypsis for salmonid fry involves their resemblance to the gravel substrate of stream or lake bottoms, then the introduction of salmonids to habitats having different substrate coloration would result in greater predation mortality for introduced than for native species which have coevolved with predators in that habitat.

Juvenile salmonids exhibit convergence on "stream coloration" (Nikolsky 1963) with countershading (Thayer 1909) and parr marks (melanin bars or blotches) on their lateral sides (except pink salmon, *O. gorbuscha*). Donnelly and Dill (1984) showed the silvery sides and ventrums of parr reflect substrate spectral characteristics (achromatic reflectance), so that their lateral sides are similar in wavelength and intensity to most gravel of a given colour, but darker substrate particles absorb light. The melanin of parr marks absorbs light, thereby enhancing the resemblance of parr to the gravel substrate. These attributes fulfill the morphological convergence criteria and provide a mechanism by which crypsis is obtained (see Donnelly and Dill 1984). Salmonid parr also exhibit numerous behaviour patterns facilitating crypsis, such as dart and freeze escape behaviour (e.g., Donnelly and Dill 1984), which would be maladaptive if fish failed to resemble their backgrounds. Thus, behavioural convergence was demonstrated as well.

The costs of production of parr or smolts in a hatchery are approximately $2.50–$5.00 per fish, but while hatchery survival is high, numerous problems beset transplanted salmonid species (trout, charr and Pacific salmon). Transplant failure has been well documented (Helle 1981; Bachman 1984) but has not been adequately explained; the majority of fish simply disappear (Webster and Flick 1981) necessitating frequent reintroductions (Bachman 1984). Proposed explanations of the losses include competition with native trout (Schuck 1948; Miller 1954; Symons 1969), lack of suitable overwintering habitat (Shetter and Hazzard 1941; Shetter 1947), and selection for maladaptive behaviours in hatcheries (Vincent 1960; Fenderson et al. 1968; Symons 1969; Fenderson and Carpenter 1971; Jenkins 1971; Ruggles 1980; Bachman 1984; Swain and Riddell 1990). Wild fish have been assumed to have a survival advantage over domestic stocks (Flick and Webster 1964) but equivocal results suggest that other factors might be affecting transplant survival (Webster and Flick 1981). We hypothesized that hatchery fish might colour-acclimate to receiving tanks making them vulnerable to predator visual detection even when reintroduced to the stream where they originated.

Sumner (1934, 1935a,b) showed that mosquitofish (*Gambusia affinis*) successfully colour acclimated to tanks within several weeks and that colour acclimated fish had a 2:1 survival advantage compared to non-acclimated fish when subjected to predation by bird or fish predators. Donnelly and Whoriskey (1991) used similar techniques and hooded merganser (*Lophodytes cucullatus*) predators to determine the survival advantage of cryptic coloration for brook trout (*Salvelinus fontinalis*) preyed upon in stream channels having a gravel substrate. They found a 1.7:1 advantage for cryptic compared to contrasting trout. This result demonstrated the survival value of salmonid crypsis against the appropriate background. Subsequent experiments showed that predator-naive brook trout colour acclimated for crypsis had similar survival rates to colour mismatched fish that had previously survived merganser predation trials (W. A. Donnelly, unpublished data). This finding suggests the equivalence of colour acclimation to predator conditioning (and selection) for reducing predation risk of brook trout. The first objective of our present study was to test whether a similar survival advantage could be obtained by colour acclimating Atlantic salmon (*Salmo salar*) for crypsis. However, the effect of having no gravel substrate in the predation arena was tested. Parr markings could only serve to render the fish cryptic over gravel. By testing colour acclimated fish with parr marks in arenas without gravel, we could evaluate the role of parr marks in crypsis (i.e., test for Suffert's third criteria).

Predation is important for salmonids in the wild. Planted fingerling trout often do not survive for long if they are introduced to streams already containing trout (Needham and Slater 1944; Needham 1947; Miller 1954). Mills (1964) showed heavy predation by trout on stocked salmon for the first few days after transplantation and suggested that it would be desirable to empty streams of trout prior to introducing salmon. Avian predators also hit juvenile salmonids hard (White 1936; Sayler and Lagler 1940; Huntsman 1941; Elson 1962; Wood 1987) and bird control has been employed to decrease predation on Atlantic salmon populations (Huntsman 1941; Elson 1962). However, no good evidence exists showing that bird control increases fish production and predator control likely is only a short term solution because removed birds are soon replaced by others (Draulens 1987).

Our second objective was to evaluate a suggested (Donnelly and Dill 1984) genetic component to crypsis, by quantifying predator selection of colour-related traits of Atlantic salmon and rainbow trout (*Oncorhynchus mykiss*) in two rivers (the Satarouski and du Gouffre Rivers) where these fish had been introduced in the past 5–10 years. We reasoned that the relatively recent introduction of non-native species to these rivers would reveal directional selection on their coloration compared to native species which were assumed to have been selected for cryptic coloration and have stable trait distributions. Colour differences between native fish and the offspring of introduced fish hatched and reared in the wild will be due to genetic factors and not to inappropriate colour acclimation. In sympatry, brook trout and native Atlantic salmon are generally similar in colour, size and morphology (Maitland et al. 1981). In our work native brook trout coloration served as the model that the introduced stock was predicted to converge on. Comparison with other sympatric species allows determination of the degree of convergence between native species on cryptic coloration in similar habitats under similar predation risk. The difference in coloration between introduced species and native species versus the convergence of native species on similar coloration reveals the degree to which predator based selection operates on the introduced stock to produce convergence on cryptic morphs. Differences in frequencies of predator inflicted scars from previous captures by predators (White 1936) were used to quantify the magnitude of predation risk experienced by introduced salmonids compared to native brook trout.

Materials and Methods

Laboratory Experiments

Atlantic salmon alevins (500) were obtained from the provincial government hatchery at Anse Pleuruse on the south shore of the St. Lawrence River and transferred to the Macdonald campus of McGill University. The fish were installed in a blue-bottomed refrigerated tank for 4 days and subsequently were transferred to either brown or tan stream channels (described in Donnelly and Whoriskey 1991) to colour acclimate for several weeks. The stream channels had a large surface area with a mild current and the fish during acclimation were able to familiarize themselves with the arena where the mergansers would prey upon them. Refrigerated water was supplied to the channels by a semi-flow-through system from two refrigerated tanks. Water temperature was maintained at 12°C. The salmon were fed approximately eight times daily and the stream channels were cleaned twice daily using fine-meshed nets to remove excess food and wastes. No gravel was used in the stream channel in order to test the effect its absence would have on salmonid crypsis. Diatom filters were used daily to scrub the water and reduce turbidity in the channels.

The two merganser predators were held with a large number of overwintering waterfowl in an adjacent room. They were fed occasional Atlantic salmon and a steady diet of Purina Protein Plus dog food ad lib. The birds were food deprived 5 h prior to each predation trial.

The predation trials were begun 130–160 days after colour acclimation began when salmon averaged approximately 60 mm SL. Before each trial, 15 salmon of each colour-acclimation group (brown and tan) were randomly netted and the pelvic fin was clipped to indicate whether brown or tan acclimation occurred. The remaining fish were netted from the stream channel and placed in a refrigerated holding tank until the trial was completed, when they were returned to the stream channel they had previously occupied. The channel that did not serve as the predation arena was covered with metal shelving to protect its contents and to give the mergansers an area to rest between foraging bouts. The colour acclimated fish with clipped pelvic fins were introduced to the stream channel where the predation trial would occur and the two mergansers were transferred by net to the predation arena and allowed 1 or 2 h to prey on the 30 test salmon. At the completion of the predation trial the surviving fish were netted out of the stream channel, counted and identified to their colour-acclimation group. Surviving fish were transferred to an individual (22 L) tank in a walk-in cooler for 2 days to determine the delayed mortality rate (due to injuries) following the trial.

Between February 27 and April 1, 1989, 22 predation trials were done, 11 for each channel colour. Trials were at first 2 h duration; however, due to increased success by the mergansers as they grew more experienced, trial length was reduced to 1 h. Trials were alternated between brown and tan channels on successive trials. After several trials it was recognized that brown acclimated fish were experiencing greater predation than tan acclimated salmon regardless of stream channel colour. Batches of 30 brown and tan acclimated fish were weighed to determine if a size difference might explain this bias.

Results were analysed for the number of fish eaten, the number of fish that subsequently died due to injuries, and these two categories were pooled for each fish colour using *t*-tests or a binomial test with $\alpha = .05$.

Field studies

The study rivers — The Satarouski River is a tributary of the Cartier River in Cartier Park (north of Quebec City). Both the Cartier and Satarouski have peat-stained water and dark-brown gravel substrate. Since 1981 Atlantic salmon have been transplanted to various locations in the Cartier to replace the native run extirpated more than 50 years ago (Dulude and Vallières 1986). More than half a million Atlantic salmon were introduced by 1989, including 439 290 alevins, 86 400 smolts and 18 000 adult salmon (Dulude 1990) but success measured in numbers of returning adult fish were disappointing. Total returns to 1989 numbered 1 639 adult fish. A conservative estimate is that each returning adult spawner has cost slightly over $800.00 to produce. Atlantic salmon usually spend 2 or more years in freshwater, thus the damage that predators can potentially inflict on a cohort is greater than for most Pacific salmon who leave fresh water after a year or less (Ricker 1972).

The du Gouffre River is a clear water stream in Charlevoix County east of Quebec City. It generally has light coloured gravel, but darker substrate is present in its upper tributaries. It contains native Atlantic salmon and brook trout as well as self-introduced rainbow trout (likely from Great Lakes enhancement projects) which established themselves in its upper tributaries (Dulude 1986). The rainbow trout in the du Gouffre River are presently confined to headwater tributaries only (la Mare River and Remi Creek) where brook trout co-occur. Atlantic salmon are sympatric with brook trout in the main river but not in the tributaries having rainbow trout.

Fish in the two experimental rivers were captured in August 1987 with Quebec Ministry of Leisure, Hunting and Fishing (MLCP) assistance using standard MLCP sampling techniques. Fish were taken by electrofishing for 20 min in areas where juveniles of the introduced species had been sampled previously. The small sample sizes in our study are due to the sampling regime employed. Sampled fish were held in white plastic buckets for approximately 30 min after capture (thus all fish were lighter in coloration when photographed than they would be in the river), photographed with 325 mm and 76 × 7 cm cameras and returned to the river.

Measuring Fish Coloration

Coloration of native and introduced fish was documented using photographic methods for recording lateral patterns and dorsal as well as lateral coloration. Diapositives (35 mm, Ektachrome 400 ASA) of the dorsums and lateral sides of fish of each species sampled were taken against white brackgrounds for each river using natural lighting, however the spectra of the backgrounds differed for the two rivers. Closeup lenses were used to increase image size for fish sampled in the du Gouffre River, but no closeup lenses were available for the Satarouski River sampling. A plastic rule against the white background adjacent to fish permitted measurement of sampled fish to the nearest mm (SL).

Diapositives were analyzed by projection on a viewing screen and using a photographic spotmeter to measure reflectance and coloured filters to measure spectral distribution of various areas of fish, but especially the dorsums due to the predominance of bird compared with fish predators in headwater streams and rivers (see Egglishaw and Shackley 1985). Blair (1947) used a photographic reflectance meter equipped with red, blue and green filters to obtain spectral reflectance in his studies on mice coloration. A problem associated with using a standard photographic reflectance meter are its wide angle of light acceptance which introduces imprecision when focussing on discrete areas. Fitted with coloured filters (red, blue, yellow, and orange Vivtar; green was obtained by superimposing blue and yellow filters) spotmeters can be used to measure the spectra of fish (or other objects such as gravel) either in the field, or of objects recorded on projected 33 mm diapositives. In this study, the spectral reflectance of projected diapositives of introduced species was compared to native brook trout. Native dace (*Rhinichthys* sp.) in the Satarouski River and Atlantic salmon in the du Gouffre River were also compared to brook trout to determine the degree of convergence of sympatric species on similar coloration. Spectral measurements were used to infer how suitable the coloration of the introduced stock was with respect to the gravel substrate by their similarity to native brook trout. Therefore the difference between the introduced species and brook trout was taken for tabular comparisons. If the introduced species had a lighter dorsum and native brook trout were darker, a positive difference would be obtained. If the introduced species were darker than the native species, a negative value would be obtained.

On individual diapositives, the background reflectance was taken with no filter and then with coloured filters to derive background values for discrete wavebands. If fish are being compared on a single diapositive, no differences in background reflectance should be found across the diapositive. If differences do exist, measurement of background reflectance adjacent to the target can correct for background differences on the diapositive. Because targets may vary in reflectance from one skin area to the next (for example, across the dorsum), spotmeter values were recorded as ranges rather than averaged. Measurements were taken as the range (minimum to maximum value, measured in ev, electron volts). The lower value obtained (minimum reflectance) was used for calculations involving backgrounds and targets to correct for physiological colour changes that occurred in the white buckets before the fish were photographed. Targets included dorsums, parr marks, lateral sides and ventrums of fish. If targets with backgrounds having different spectral qualities are compared, or if a large difference exists for background reflectance on different diapositives, inherent contrast should be calculated. This value is the illumination of the target (L) minus the illumination of the background (L′) divided by the illumination of the background ($(L-L')L'^{-1}$; see Ware 1973) for each of the wavebands measured. This calculation was done in our study for comparing brook trout from the Satarouski River to those from the du Gouffre River because diapositives of fish were taken against two different white backgrounds. For most of our work, the reflectance of the target was subtracted from the background reflectance (L'-L; this corrects for filter density differences) and the differences obtained between fish were directly compared in ev absorbance units. While this technique provides only a relative measure, it is a close enough approximation to inherent contrast provided the difference in reflectance of the backgrounds on different diapositives is equal to or less than approximately 1 ev. Background reflectance (L') is reported for each fish analyzed in this manner. Because fish could darken or lighten as they grow, standard length is reported as well. Once data are obtained, a matrix taking the absolute difference between the values for different species can be constructed or, alternatively, the values obtained can be plotted graphically. For graphs, reflectances without filters are plotted (overall reflectance or absorbance compared to the background), and spectral plots begin at blue and end with red. Values for individual fish or ranges were plotted rather than using means so that some idea could be obtained of the variance in spectral characteristics. Given the same background reflectance on diapositives it is also possible to obtain the difference in reflectance between native species and introduced species (or two native species to test for convergence) by subtraction and plot this value. Thus either species becomes the zero baseline and the values represent the mismatch between the two species for the area measured in the different spectral regions.

Additional Photographic Methods

Besides the 35 mm photographs taken for spectral analysis, larger format diapositives were taken with a Mamiya RB67 (6 × 7 cm diapositives) using a photographic chamber having mirrors which allowed both sides of 36 fish to be captured in a single frame (described in Donnelly 1985). A dissecting microscope was used for taking counts of parr marks (counted from the operculum to the posterior insertion of the adipose fin) and length measurements (SL) were obtained using an eyepiece micrometer for each fish on the diapositives. Results were analyzed using *t*-tests with $\alpha=0.10$ due to small sample sizes (e.g., Peterman 1990)

Predation Risk

We also used the number of bird marks (White 1936) on the sides of sampled fish to infer predation risk of introduced compared to wild species. The number of fish bearing marks from previous predation attempts should be approximately equal for both wild and introduced species if they are equally likely to be seen, captured and escape. If more introduced fish in equal-sized samples are first marked, then their predation risk is presumed to be greater. Predation risk (PR) for the introduced stock in a sample can therefore be represented as:

$$PR = \frac{I_m / I_t}{W_m / W_t}$$

where I_m is the percentage of introduced fish having marks, I_t is the total sample size of the introduced species, W_m is the percentage of wild fish marked (of a single native species, i.e., brook trout), and W_t is the total number of wild fish sampled. Statistical significance of the data was determined using chi-square. The value of PR should usually exceed unity (see Appendix 1 for possible exceptions) and a PR value of 2.0 would indicate that predation risk for the introduced stock is twice that of the wild stock.

Results

Laboratory experiments

Overall 235 Atlantic salmon fry were eaten by the mergansers during the 22 trials. An additional 22 fish died subsequently due to injuries sustained in the trials. More fish were eaten in the brown channel ($n=144$) than the tan channel trials ($n=91$) ($x^2=11.95$, $P<0.001$). The total number of fish eaten during the trials or dying following the trials increased with successive trials suggesting the mergansers learned to be more effective predators. Brown acclimated fish experienced greater predation than tan acclimated fish in both tan and brown stream channels. Tan acclimated fish were found to weigh approximately 14% more ($x=5.72$ g) than brown acclimated salmon ($x=5$ g).

Analysis of the results of predation experiments in the tan stream channel showed that less than one quarter ($n=16$) of the cryptic tan acclimated salmon were eaten compared to the contrasting brown acclimated fish ($n=75$); this difference was highly significant ($x^2=38.25$, $P<0.001$). More cryptic fish ($n=3$) died in the two day recovery period compared to mismatched salmon ($n=0$) but the difference was not significant. The pooled results (eaten + died) for the tan-acclimated salmon revealed that tan-acclimated cryptic fish had a highly significant survival advantage compared to the colour-mismatched brown acclimated fish ($x^2=33.36$, $P<0.001$).

In the predation trials in the brown stream channel, significantly more ($x^2=13.44$, $P<0.01$) brown acclimated salmon were eaten ($n=94$) than colour mismatched tan fish ($n=50$). Post-trial mortality did not differ significantly (binomial test, $P=0.5$) for brown ($n=9$) and tan acclimated salmon ($n=10$). Pooling the number of fish eaten and dying subsequently, the cryptic brown-acclimated fish had a significant survival disadvantage in the brown channel (103 were eaten or died) compared to mismatched tan acclimated salmon (60 were eaten or died)($x^2=11.34$, $P<0.001$).

Field studies

The mixed stock of Atlantic salmon introduced to the Satarouski River in 1981 and 1982 still had heterogeneous coloration in August 1987. Some older parr had a single row of erythrophores along their lateral sides, others had a double row. All introduced Atlantic salmon appeared to have lighter dorsal coloration than the native brook trout, but one of the three salmon spectrally sampled had the same overall absorbance as the brook trout (Fig.1, triangles, no filter). The dorsum of the native brook trout reflected green, orange and red in approximately equal amounts (troughs of spectral absorbance) and absorbed more blue and yellow (peaks). The Atlantic salmon dorsal spectra were similar, but none of the three salmon matched the brook trout in the blue, green or yellow portions of the spectrum, one matched in the orange, while two matched in the red. Brook trout had fewer and larger parr marks than the introduced salmon ($P<0.025$, *t*-test) but were not significantly different in standard length ($P>0.1$, *t*-test, see Table 1).

Greater predation intensity on the introduced Atlantic salmon than native brook trout was evidenced by bird mark scars (White 1936) visible on 17 Atlantic salmon fry and parr (I_t=29); only 2 brook trout sampled in the same locations had similar capture marks (W_t=10). Predation risk for the introduced salmon was therefore estimated to be almost three times the corresponding risk for brook trout (PR=2.93) (x^2=6.0, $P<0.02$). Eight common mergansers and a belted kingfisher were observed fishing on the Satarouski River after our sampling.

Some Atlantic salmon introduced to the Cartier River only two weeks previous to sampling were poorly matched to the colour of the native brook trout and dace. The salmon sample was small (*n*=2) and only one of the fish was positioned so it could be analyzed spectrally, but it mismatched the brook trout for every waveband whereas the reflectance of brook trout and dace was similar for all wavebands but yellow. Large groups of mergansers had also been observed fishing where these fish were introduced (P. Dulude, MLCP, personal communication).

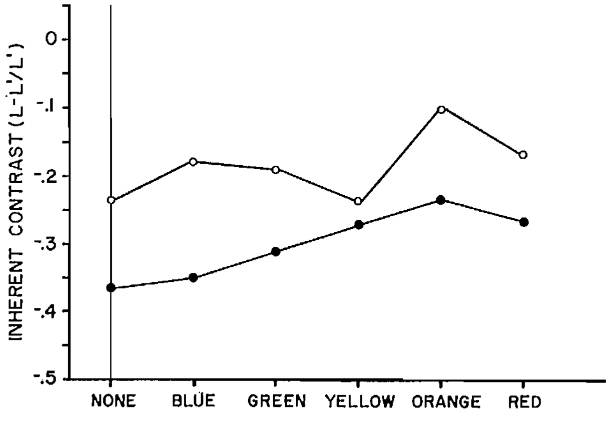

FIG. 1. Spectral distribution in ev (electron volts) absorbance (L'-L) for three introduced Atlantic salmon and a native brook trout sampled in the Satarouski River. The introduced salmon are represented by open circles (90 mm; L'=7 1/3 ev), triangles (60 mm; L'=7 1/3 ev) and diamonds (54 mm; L'=7 ev), the native brook trout is represented by filled triangles (94 mm; L'=7 1/3 ev).

TABLE 1. Parr mark numbers and fish size differences in the Satarouski and du Gouffre rivers.

	Parr mark		Fish length		
	Mean	Variance	Mean	SD.	*n*
Satarouski					
Brook trout	7.7	1.233	48.8	3.36	10
Atlantic salmon	8.6	1.190	51.2	9.70	29
du Gouffre					
Brook trout	7.3	0.599	67.4	2.13	16
Atlantic salmon	7.9	0.863	52.4	12.15	23

The dorsal coloration of both native salmonids (Atlantic salmon and brook trout) sampled in the du Gouffre River was highly reflective presumably to allow them to escape predator visual detection against the light-coloured substrate. Ranges of dorsal spectral absorbance of native brook trout and Atlantic salmon are shown in Fig.2. The spectrally sampled brook trout (*n*=3) had similar maximum absorbance values (no filters) to Atlantic salmon (*n*=4), but the minimum values showed that brook trout (*n*=3) were somewhat darker. This may be due in part to the fact that brook trout had vermiculations on their dorsums while Atlantic salmon had large discrete dorsal blotches, and it was the area between blotches on salmon that was spectrally sampled. The dorsums of brook trout were more variable than those of salmon in the blue end of the spectrum, but both species ranges for green were identical. Atlantic salmon dorsums absorbed more yellow and orange, while brook trout dorsums absorbed more red than Atlantic salmon. Dorsal spectral distribution variability was greater for the brook trout than the Atlantic salmon but overall the coloration of the two species was very similar. Table 2

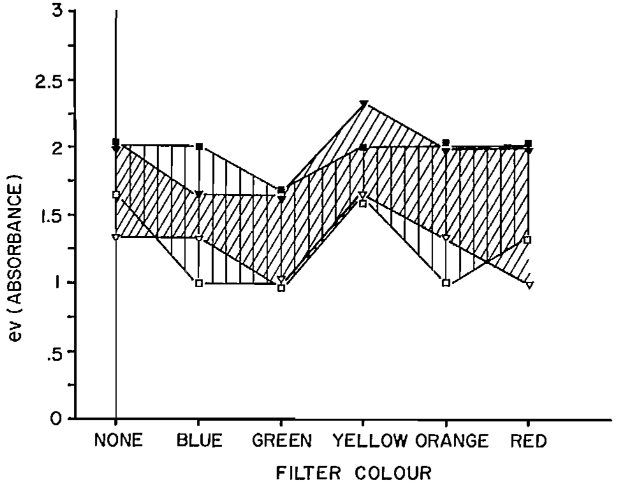

FIG. 2. Maximum (filled inverted triangles) and minimum values (open inverted triangles) obtained for dorsal spectra of native du Gouffre Atlantic salmon taken from 2 different diapositives (94 and 44 mm; L'=6 1/3 ev), (120 and 50 mm; L'=6 2/3 ev) compared with maximum (filled squares) and minimum values (open squares) for 3 native brook trout (134 mm; L'=7 1/3 ev, 110 mm, L'=7, 129 mm, L'=7).

TABLE 2. Differences (units are ev) against a uniform white background between native brook trout and introduced rainbow trout coloration. Negative values indicate the rainbow trout were uniformly darker than the brook trout.

	Area measured				
Filter colour	Parr marks	Inter-marks	Dorsum	Ventrum	Total
1. None	-1 1/3	-1.0	-1 1/3	-1 1/3	-5.0
2. Blue	-1 1/3	-1 1/3	-1 2/3	-1 1/3	-4 2/3
3. Green	-1 1/3	-1.0	-1 1/3	-1.0	-4 2/3
4. Yellow	-1 2/3	-1 1/3	-1 1/3	-1 1/3	-5 2/3
5. Orange	-1 1/3	-1 1/3	-1 2/3	-1 2/3	-6.0
6. Red	-2.0	-1 1/3	-1 1/3	-1.0	-5 2/3
7. Total	-9.0	-7 1/3	-8 2/3	-7 2/3	-31 2/3

shows how a rainbow trout and a brook trout of similar size, sampled at the same site in the upper tributaries of the du Gouffre River, and photographed on the same diapositive compared in coloration for various areas of their bodies. The parr marks, lateral side and ventrum of the native brook trout were equally or more reflective (no filter) than the background. Spectrally only the dorsum and orange and red wavebands of the parr marks of the brook trout were less reflective than the white background. The same areas of the self-introduced rainbow trout absorbed light of all wavebands. The introduced rainbow trout had substantial mismatch compared to the brook trout (Table 2); the greatest mismatch was found for parr marks and dorsal coloration. Spectrally the greatest mismatch occurred for longer wavebands (red, orange and yellow). The total mismatch of all areas was substantial, suggesting that the introduced rainbow trout have not yet had sufficient predator selection to converge on the native brook trout coloration. Brook trout in the main river had fewer and larger parr marks ($P<0.025$, *t*-test) and greater standard lengths ($P<0.001$, *t*-test) than the native Atlantic salmon (Table 1). The beak mark data suggested that the self-introduced rainbow trout were experiencing greater predation than native brook trout, however the samples were small (2 of 4 fish were marked, compared to 2 of 6 brook trout sampled in the same locations (PR=1.50)).

The inherent contrast spectra of native brook trout from the Satarouski and du Gouffre Rivers are compared in Fig.3. Although both species are native to their respective rivers, large differences in dorsal reflectance exist, and the spectral characteristics of the dorsums are different as well. Size differences were significant between the brook trout in both rivers ($P<0.001$, *t*-test), but no significant differences existed between the two rivers in brook trout parr mark number ($P>0.1$, *t*-test). No size differences existed between the Atlantic salmon in the two rivers, but parr mark number was significantly different ($P<0.01$, *t*-test).

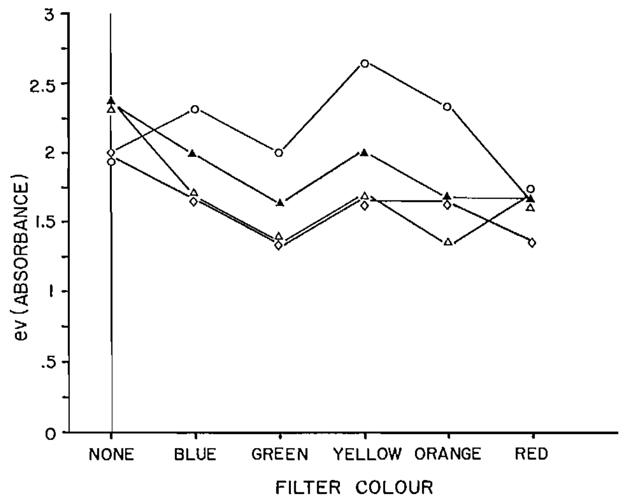

FIG. 3. Inherent contrast spectra for dorsum of native brook trout from the du Gouffre River (open circles, 134 mm, L′=7 1/3 ev); compared with native brook trout from the Satarouski River (filled circles, 94 mm, L′=7 1/3 ev). Inherent contrast was used because the backgrounds used when photographing the fish differed spectrally. L=illumination of dorsum. L′=illumination of background.

Discussion

In contrast to our laboratory experiments with brook trout (Donnelly and Whoriskey 1991), the survival advantage of colour-acclimation for crypsis in Atlantic salmon is inconsistent. Our results suggested that colour acclimated Atlantic salmon gained survival advantages only over light coloured backgrounds; acclimation for crypsis improved the survival of tan but not brown acclimated fish. One possible explanation for this result may have been the size difference discovered between the tan and brown fish (likely due to improved feeding for tan acclimated salmon due to the greater contrast of fish food in the tan channel compared to the brown channel, e.g., Ware 1973). This resulted in mergansers capturing the smaller, slower brown acclimated salmon.

Another explanation is that the salmon used for the predation experiments were incapable of acclimating effectively to the dark background of the brown channel. Even when they were fully acclimated, they may have retained coloration more similar to the tan channel than the brown channel. However, mosquitofish were better able to colour acclimate to dark than light colour backgrounds (Sumner 1934a, 1935a,b), as were brook trout (Donnelly and Whoriskey 1991). However in the present work tan acclimated salmon were less likely to be eaten or captured than the brown acclimated fish regardless of background colour. This suggests that species or stock specific, genetically based colour differences may exist. Stock specific characteristics are well known among salmonids (Ricker 1972; Riddell and Leggett 1981; Riddell et al. 1981). Stock related colour differences have been found between juveniles from populations of coho salmon (Donnelly 1985) and chinook salmon (Taylor and Larkin 1986) so colour-acclimation may only result in a partial resemblance to any background colour. The fidelity of the resemblance obtained may depend on how closely the fish resembled the background to begin with.

The proximal explanation for why brown acclimated salmon experienced greater predation than tan acclimated fish is that tan acclimated fish developed reflective lateral coloration and nearly lost their parr marks, whereas brown acclimated fish develop darkly pigmented parr marks and darker lateral sides. Salmonid parr marks were hypothesized to render salmon parr cryptic when viewed against gravel backgrounds because they simulate a heterogeneous gravel substrate (see Donnelly and Dill 1984); parr were hypothesized to lose their parr marks (or have none at all in the case of pink salmon) when in a pelagic environment because dark lateral blotches detract from the resemblance of fish to the background. The absence of gravel in the stream channels favored the tan-acclimated fish whose reflective lateral sides and indistinct parr marks enabled them to escape visual detection by achromatic reflectance in both brown and tan channels, whereas the brown acclimated fish with dark parr marks against the same backgrounds were more visible when viewed laterally by the mergansers. Mergansers are visual predators and pursue prey under water (Lindroth and Bergstrom 1959). Perhaps our results would have been different had a strictly aerial predator been used, or had the stream channels contained gravel substrate as in our experiments using brook trout. These experiments showed that brown acclimated brook trout have significantly more parr marks than tan acclimated fish (Donnelly, unpublished data). Comparing our results for brook trout in channels having gravel substrate (Donnelly and Whoriskey 1991) to the results obtained for Atlantic salmon in channels having no gravel serves to demonstrate Suffert's third criteria of protective resemblance; parr marks protected juvenile salmonids over gravel backgrounds but failed to protect strongly parr marked fish when no gravel substrate was present.

Results from the field work are based on small sample sizes, and must be interpreted with caution. However, they suggest that in both sampled rivers the coloration of the introduced species differed from that of the native species to a greater extent than native species differed among themselves. In the dark coloured Satarouski River the mixed stock of introduced Atlantic salmon was generally lighter than the native brook trout. In the du Gouffre River with its mostly light coloured substrate, the introduced rainbow trout were darker than the native brook trout and Atlantic salmon. In addition the native brook trout in both rivers differed from native and introduced Atlantic salmon in terms of parr mark number. Donnelly (1985) showed that coho parr mark number and form (length, width and intermark width) varied both between and within four streams sampled in Southwestern British Columbia, and Taylor and Larkin (1986) showed that dorsal coloration and parr mark characters of chinook salmon (*O. tschawytscha*) varied between British Columbia streams. While parr mark variation is assumed to be adaptive, parr mark size correlated poorly to gravel substrate size (Donnelly 1985). Nevertheless, in merganser selection experiments over gravel and bare substrates, coho parr mark number and standard length were shown to undergo directional selection which differed between the backgrounds (Donnelly 1985). In both study rivers, the introduced species had more scars on their bodies inflicted by predators in previous captures than the native brook trout sampled at the same locations. In the field studies, scar counts (equivalent to predation risk or survival disadvantage) was nearly 3:1 for introduced Atlantic salmon in the Satarouski River, and 1.5:1 for rainbow trout in the du Gouffre River compared to the native brook trout. Because species such as mergansers congregate in favourable feeding areas, higher than average mortality is expected in outplanted hatchery fish (Wood 1987), and this would be especially true if transplanted fish were more easily detected by visually searching predators due to inappropriate coloration. Crypsis breakdown of introduced salmonids may facilitate predator removal of conspicuous fish at higher rates than native species for years and perhaps decades if a genetic component to crypsis exists. Crypsis breakdown whether due to nurture, nature or both may explain the general lack of success in transplanting of salmonids to new habitats (Helle 1981; Webster and Flick 1981; Bachman 1984).

In the short term, reproduction by transplanted fish will produce a range of phenotypes on which predator selection can operate. Some phenotypes will be less cryptic in that particular habitat and since predators are more likely to remove conspicuous fish than those that are cryptic, gradually the population mean should shift to more cryptic coloration. Introduced populations of fishes will thus experience increased predation risk due to crypsis breakdown until their coloration is equally cryptic as that of the native stock. Since introduced fish may be bearing two or more times the predation load of the wild population, their reproductive potential should be two or more times that of native species or they should be introduced in extremely large numbers if we are to reasonably expect them to establish themselves. To minimize the risk of predation for transplants, one could introduce fish closely matching the background coloration of the new habitat. Methods of colour-matching of fish in habitat include taking spectral maps of the coloration of the substrate where the fish will ultimately be transplanted and locating a stock having the appropriate coloration to be cryptic against this background. Alternatively, matching the coloration of the stock of fish to be introduced to the spectra of closely related native species in the recipient waters may be equally successful. Colour acclimation of salmonids in the hatchery for a few weeks prior to their release may also enhance the cryptic resemblance of fish prior to their introduction to new habitats. Introducing a mixed stock such as was done in the Satarouski River will increase the likelihood of having cryptic phenotypes represented, however fish preadapted for crypsis may not be present in sufficient numbers to establish self-sustaining populations, and offspring of conspicuous fish that survive to reproduce with cryptic phenotypes will be less cryptic than if a single colour-matched stock is transplanted. In spite of measures that can be taken to reduce crypsis breakdown it is unlikely that transplants will be an ideal match in comparison to native fishes whose cryptic resemblance has been honed by predator selection.

Homing in salmonids has received a great deal of attention in the past, and has been primarily concerned with questions concerning whether and how. Not much attention has been given to why (Ricker 1972). Authors such as Hasler et al (1976) have interpreted homing as being advantageous, but it is possible that the disadvantages of wandering may better explain the evolution of this adaptation. The offspring of salmonids which fail to return to their natal streams to spawn may experience similar problems as fish transplanted by man; high predation rates attributable to crypsis breakdown. Homing fishes thus provide cryptic resemblance to their offspring and advantages in eluding predator visual detection and capture compared to wanderers. A crypsis (sic) advantage may favour evolution of homing in salmonids.

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Appendix 1

Cases are rare where the value of PR could be less than unity. This might occur if size-selective predation was occurring, (i.e., predators were unable to capture the introduced fish as well as the wild fish), if the introduced fish were less profitable or less preferred prey and given less attention by predators, if the introduced stock were preying on the wild stock to a greater extent than the converse (and they made similar marks to bird predators), or if an environmental change occurred which changed the spectral properties of the background and made the native stock more visible top predators than the introduced stock (unlikely). We assume that the introduced and wild stock are equally likely to escape from a predator after being seized and thus bear the scars which are used to derive PR and would have similar mortalities given similar predation stress. The assumptions are unlikely to affect the interpretation of greater predation rates on introduced fish since wild stocks should have coevolved with the predator and therefore have adaptations which make them more likely to escape after having been captured than the introduced fish. Thus native species would be more likely to bear predation, and the PR would underestimate the actual rate of predation on the introduced stock.

Effects of Aerial and In-Stream Threat of Predation on Foraging by Juvenile Atlantic Salmon (*Salmo salar*)

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In this study, foraging juvenile Atlantic salmon (*Salmo salar*) were exposed separately to an aerial or in-stream threat of predation, in the form of a stuffed belted kingfisher (*Ceryle alcyon*) or a cast of an adult brook trout (*Salvelinus fontinalis*), or to an overhead and in-stream disturbance in the form of a bird-shaped or fish-shaped model. The response to both predators, and to a simple overhead and in-stream disturbance, were compared. In all cases, juvenile salmon took significantly longer to resume foraging following exposure to the kingfisher model. There was no significant difference in the time taken to resume foraging, following exposure to the trout model or an overhead disturbance. An in-stream disturbance had the weakest effect on salmon foraging. Salmon reduced the distance they travelled to capture a prey item following exposure to either the kingfisher or bird-shaped model. In contrast, there was no difference in the distance fish travelled to capture a prey item following exposure to the trout or fish-shaped model as compared to that travelled prior to exposure to either of these two models. Finally, juvenile salmon only showed a distinct escape response following presentation of the kingfisher model. Our results suggest that juvenile Atlantic salmon from the Miramichi River, New Brunswick, Canada, discriminate between both aerial and in-stream predators, and other general disturbances.

Dans notre étude, des saumons atlantiques juvéniles en période d'alimentation ont été exposés séparément à une menace de prédation dans l'air ou dans l'eau, sous la forme d'un spécimen empaillé de martin-pêcheur d'Amérique (*Ceryle alcyon*) ou d'un moulage d'un omble de fontaine adulte (*Salvelinus fontinalis*), ou à une perturbation par les airs ou dans l'eau sous l'espèce d'un modèle ayant la forme d'un oiseau ou d'un poisson. Les réactions aux deux prédateurs, et à la simple perturbation dans les airs et dans l'eau, ont été comparées. Dans tous les cas, les saumons juvéniles ont mis nettement plus longtemps à recommencer à s'alimenter après l'exposition au martin-pêcheur. Il n'y avait pas de différence significative dans le délai avant la reprise de l'alimentation après l'exposition au modèle de l'omble de fontaine ou à une perturbation par les airs. C'est la perturbation dans l'eau qui avait l'effet le plus faible sur l'alimentation des saumons. Les saumons réduisaient la distance parcourue pour capturer une proie après exposition soit au martin-pêcheur soit à la forme d'oiseau. Par contre, il n'y avait pas de différence dans la distance parcourue pour capturer une proie après l'exposition au moulage de l'omble ou au modèle en forme de poisson par rapport à ce qui se passait avant l'exposition à l'un de ces deux modèles. Enfin, les saumons juvéniles n'ont montré une nette réaction de fuite qu'après la présentation du martin-pêcheur empaillé. Nos résultats semblent indiquer que les saumons atlantiques juvéniles de la rivière Miramichi (Nouveau-Brunswick, Canada), font une discrimination entre les prédateurs présents dans l'air et dans l'eau, et autres perturbations d'ordre général.

Introduction

Along with the direct effect predators can have on prey by reducing their numbers, recent work has demonstrated that the risk of predation can also significantly affect prey growth rate and survival by influencing various aspects of prey behaviour, such as habitat selection and foraging activity (Dill 1987). In many cases, the presence of, or exposure to, a predator results in a decrease in energy intake by the prey (Dill 1983; Heads 1986; Magnhagen 1988; Gotceitas 1990). For example, a number of studies with several different salmonids have shown that fish vulnerable to predation significantly reduce their foraging activity following exposure to a predation threat (Dill and Fraser 1984; Grant and Noakes 1987; Metcalfe et al. 1987; Huntingford et al. 1988). In these studies, test fish were exposed to a predation threat from a potential in-stream predator, a larger salmonid. However, fish are not the only predators of juvenile salmonids, as a variety of birds (White 1936; Elson 1962; Wood 1987) and some mammals (Heggenes and Borgstrom 1988) are also known to feed on these fish. Although work with other taxa has shown that prey will respond differentially to different predators (Walther 1969; Turner 1973; Hirsch and Bolles 1980; Webb 1982; Foster and Ploch 1990; Magnhagen and Forsgren 1991), no study has looked at the response of juvenile salmonids to an aerial versus an in-stream threat of predation.

Salmonids inhabiting most lotic systems are constantly exposed to objects both drifting downstream towards them in the water column, and passing overhead above the water. Many, if not most, such objects

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are of little consequence to the fish, however, some will represent a risk of predation. Since predator avoidance typically involves a cost to the prey (Lima and Dill 1990), it would seem advantageous for prey to be able to identify predators, and discriminate between these and non-predators or predator-like disturbances with respect to their response. Therefore, this study was designed to investigate (1) the response(s) of foraging juvenile Atlantic salmon to aerial versus instream threats of predation, and (2) their ability to discriminate between potential predators and predator-like objects/disturbances.

Materials and Methods

Juvenile Atlantic salmon (4.2 – 5.7 cm SL) were collected by electrofishing from the Northwest Miramichi River, New Brunswick, Canada. Fish were brought back to the laboratory at Mount Allison University, where they were housed in a communal stream tank until being used in the experiment. Water in the holding tank was maintained at 10°C, and fish were held under a 12hL:12hD light regime. While in the holding tank, fish were fed pieces of freeze-dried ocean plankton, which were introduced onto the water surface at the upstream end of the tank. This same prey was used during the experiment.

Experiments were conducted in an experimental channel (150 × 50 cm) of a recirculating stream tank (240 × 117 × 53 cm). Water temperature and depth were maintained at 10°C and 21 cm, respectively. Mean (± 1 SE) current velocity across the width of the channel was 8.2 ± 0.9 cm/s, which is within the range preferred by juvenile Atlantic salmon (Morantz et al. 1987). Screens were placed at the upstream and downstream end of the channel to confine the test fish. A gravel pad (55 × 50 cm) was situated at the downstream end of the channel to provide a potential holding site for the fish. A piece of opaque Plexiglas (30 × 12 cm) positioned against the central partition of the stream tank and equidistant from the front and back of the gravel pad, was suspended 7 cm above the gravel to provide overhead cover for the fish. The floor of the channel upstream of the gravel pad, and the wall of the central partition of the stream tank, were marked at 10-cm intervals with black marker lines to facilitate measurement of distance along the length of the channel. An automatic food dispenser was located at the upstream end of the channel, above the water and behind a blind to hide it from the fish's view. A second blind, with a viewing slit, was attached to the glass side of the channel to allow direct observation into the channel and minimize external disturbance. A video camera was suspended over the center of the experimental channel. Operation of the camera was by remote control from behind the blind.

Each experimental trial consisted of introducing one juvenile salmon, chosen randomly from the holding tank, into the experimental channel of the stream tank and allowing it 24 h to acclimatize. During the acclimatization period, the fish was fed a total of 10 prey items, delivered one at a time onto the water surface at the upstream end of the channel. The 10 prey were presented during each of two consecutive feeding sessions, 5 prey per session. The sessions were spaced 30–60 min apart. The next day, or 'Day 1' of the experiment, the juvenile salmon was again provided with 5 prey items per session during two consecutive feeding sessions, presented in a similar manner as during the acclimatization period. However, unlike the acclimatization period, 30–60 min after the second feeding session, a third feeding session was initiated. Here 3 prey items were introduced, again one at a time, followed by the presentation of a predation threat.

In a first set of trials, the response of foraging juvenile Atlantic salmon to an aerial versus an instream predation threat was examined. During the third feeding session on Day 1 of the experiment, the test fish was exposed to either a stuffed belted kingfisher (='kingfisher model') or a cast of an adult brook trout (='trout model') (30 cm, TL). The kingfisher model simulated a kingfisher in flight (i.e., wings extended laterally) and was released from behind a blind at the upstream end of the channel, from where it would 'fly' downstream over the center of the channel along a clear monofilament guide line and out of sight again at the downstream end of the channel. The trout model was released from behind the upstream screen, from where it would 'drift' downstream (i.e., tail first) until it was on the gravel pad where it would come to rest for 5 s, and then would 'swim' back upstream and out of sight behind the screen. The trout model was suspended by monofilament lines from a clear Plexiglas track located above the experimental channel, and was moved by an electric step-motor. The kingfisher and brook trout were chosen for this experiment as they represent naturally occurring predators in the Miramichi River watershed.

Presentation of the predation threat during the third feeding session was immediately followed by the presentation of additional prey items, delivered one at a time at approximately 1-min intervals. Prey were presented until 3 additional prey had been captured by the salmon.

On the third day, or 'Day 2' of the experiment, the same protocol as on Day 1 was repeated, only this time during the third feeding session the salmon was exposed to a predation threat from that predator model not used on Day 1.

A total of 16 juvenile salmon were tested (i.e., 16 trials, each trial=acclimatization period + Day 1 + Day 2). No fish was used in more than one trial. In 8 of the 16 trials the test fish was exposed to the kingfisher model on Day 1, while in the other 8 the brook trout model was presented on Day 1. The order of model presentation (i.e., on Day 1 or 2) was assigned randomly among the 16 fish tested.

In a second set of experimental trials (n=12), examining the response of foraging salmon to exposure to a predator-like overhead and in-stream disturbance, the same general protocol as described above was followed. The difference being, that following presentation of the 3 prey items at the beginning of the third feeding session on Day 1 and 2 of the experiment, test fish were exposed to either an overhead disturbance in the form of a 'bird-shaped model' resembling the kingfisher, or an in-stream disturbance in the form of a 'fish-shaped model' resembling the brook trout.

The bird-shaped model was a piece of Plexiglas cut to an identical size and shape as the body of a kingfisher, and was coloured to match the underside of the bird. However, the bird-shaped model did not have any structures resembling the laterally extended wings of the stuffed kingfisher. The fish-shaped model was also made of Plexiglas cut to an identical size as the trout model, and was coloured to match a brook trout. Unlike the trout model, however, the fish-shaped model lacked fins and a distinct head (i.e., eyes, mouth, etc.). Both these models were presented in an identical manner as the kingfisher or trout model, and each was presented on Day 1 of the experiment in 6 of the 12 trials. Again, the order of model presentation (i.e., Day 1 or 2) was assigned randomly among the 12 fish tested. No fish was used in more than one trial.

In both sets of experiments, observations were made directly into the tank from behind the blind, and from video recordings taken from above the channel. The following data were recorded.

1) Latency (s) to resume foraging following exposure to a predation threat. This was defined as the time elapsed before the juvenile salmon captured its first prey following exposure to a predation threat. Data were compared among the four predator models (Randomized-Block ANOVA, Sokal and Rohlf 1981). Use of the same individual fish on Day 1 and 2 was corrected for by using fish as a blocking variable in the analysis. Data were $\log_{10}$ transformed to attain normality.

2) Distance (cm) travelled to capture each prey item. This was recorded for both prey captured prior to and for the 3 prey captured following exposure to a predation threat. Data obtained before (n=13 prey items) and after (n=3 prey items) exposure to a predation threat were compared (Randomized-Block ANOVA) within and among the predator models. Use of the same individual fish on Day 1 and 2 was corrected for by using fish as a blocking variable in the analysis.

3) Number of prey items ignored by the juvenile salmon before it captured its first prey following exposure to a predation threat. Data were compared among the four predator models (Fisher's exact test).

4) Whether the juvenile salmon showed a distinct escape response to a predation threat or not. The test fish was considered to have shown a distinct escape response if it sought shelter under the overhead cover or tried to escape upstream. The fish was considered not to have shown an escape response if it remained in the open on the gravel pad. Data were compared within and among the four predator models (χ^2 test).

5) The distance (cm) at which the juvenile salmon responded to the downstream approach of the trout or fish-shaped models. This was measured as the distance from the tail end of the predator model to the snout of the salmon. Data were compared between models (ANOVA). Similar data could not be collected on the kingfisher or bird-shaped models because of poor resolution of the model's image on the video recordings, as the camera was focused on the tank bottom (i.e., the juvenile salmon).

Results

There was no significant order of presentation effect (i.e., model presented on Day 1 or 2) on salmon latency to resume foraging for the kingfisher ($F_{1,14}$=0.8, P>0.39), brook trout ($F_{1,14}$=0.29, P>0.60), bird-shaped ($F_{1,10}$=2.21, P>0.17) or fish-shaped models ($F_{1,10}$=1.20, P>0.29). Therefore, data for each predator model were pooled across day of presentation in subsequent analyses. Latency until a juvenile salmon resumed foraging following exposure to a predation threat was significantly influenced by the source of the threat ($F_{2,26}$=29.78, P<0.0001). Juvenile salmon took longest to resume foraging following exposure to the kingfisher model (Fig. 1). In contrast, exposure to the fish-shaped model resulted in the shortest latency to resume foraging. There was no significant difference in latency to resume foraging following exposure to either the brook trout or bird-shaped models.

There was no order of presentation effect on whether the test fish showed an escape response to presentation of the kingfisher (χ^2=1.33, df=1, P>0.05), brook trout (χ^2=0.29, df=1, P>0.05), bird-shaped (χ^2=0.48, df=1, P>0.05) or fish-shaped models (χ^2=1.09, df=1, P>0.05). Therefore, data for each predator model were pooled across day of presentation in subsequent analyses. Following exposure to the kingfisher model, juvenile salmon showed an escape response significantly more often than expected by chance (χ^2=9.0, df=1, P<0.005). In contrast, following exposure to either the brook trout (χ^2=2.25, df=1, P>0.05) or bird-shaped model (χ^2=0.33, df=1, P>0.05), the test fish did not show an escape response more often than expected by chance. When the salmon did respond to the bird-shaped model, its response was qualitatively similar to that exhibited in response to

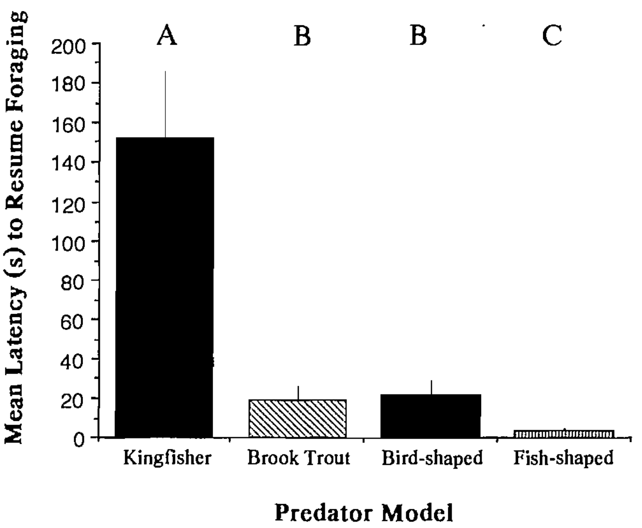

FIG. 1. Mean (+ 1 SE) latency (s) until juvenile Atlantic salmon resumed foraging following exposure to either a kingfisher, brook trout, bird-shaped or fish-shaped model. Bars with the same letter above them are not significantly different.

exposure to the kingfisher model (i.e., coming to rest under the overhead cover, or darting upstream and then remaining motionless on the bottom). Following exposure to the brook trout model, salmon either sought shelter under the overhead cover, or simply 'backed-off' (i.e., drifted slowly downstream, while continuing to face in an upstream direction) as the model approached the gravel pad and stayed behind the model while it was on the pad. Once the brook trout model started back upstream, the salmon returned to its original holding position on the gravel pad. Following exposure to the fish-shaped model, foraging juvenile Atlantic salmon showed no response to the model significantly more often than expected by chance (χ^2=8.33, df=1, *P*<0.005). Fish did initially back-off as the model approached the gravel pad, but then either stayed beside, or even moved to an upstream position, relative to the fish-shaped model while it was on the pad. The test fish resumed its original position on the gravel pad as the fish-shaped model moved upstream. Test fish showed an escape response significantly more often following exposure to the kingfisher model as compared to the brook trout (χ^2=4.26, df=1, *P*<0.025), bird-shaped (χ^2=4.23, df=1, *P*<0.025), or fish-shaped models (χ^2=11.27, df=1, *P*<0.005). There was no significant difference in the number of trials in which juvenile salmon showed an escape response when they were exposed to either the brook trout or bird-shaped model (χ^2=3.73, df=1, *P*>0.05).

There was no order of presentation effect on mean distance at which juvenile salmon responded to the downstream approach of the brook trout ($F_{1,14}$=2.09, *P*>0.17) or fish-shaped model ($F_{1,10}$=0.31, *P*>0.59). Therefore, data were pooled across days for each model in subsequent analyses. There was no significant difference in the mean (± 1 SE) distance (cm) at which the test fish responded (described above) to the downstream approach of the brook trout (49.4±3.6) or fish-shaped models (56.4±5.7) ($F_{1,26}$=1.18, *P*>0.29).

There was no order of presentation effect on the number of prey juvenile salmon ignored following exposure to the kingfisher (χ^2=0.51, df=1, *P*>0.48; Fisher's Exact test), brook trout (χ^2=0.51, df=1, P>0.48), bird-shaped (χ^2=1.20, df=1, *P*>0.27) or fish-shaped models (χ^2=1.25, df=1, *P*>0.26). Therefore, data for each predator model were pooled across day of presentation in subsequent analyses. Exposure to the kingfisher model resulted in juvenile Atlantic salmon ignoring significantly more prey items (mean±1 SE = 3.8±0.71) before capturing one, as compared to that following exposure to the brook trout (0.33±0.22) (χ^2=18.29, df=1, *P*<0.001), bird-shaped (0.5±0.23) (χ^2=11.48, df=1, *P*<0.001), or fish-shaped (0.0±0.0) models (χ^2=24.23, df=1, *P*<0.001). There was no significant difference in the number of prey salmon ignored prior to capturing one following exposure to the brook trout versus bird-shaped (χ^2=0.78, df=1, *P*>0.38) or fish-shaped models (χ^2=2.52, df=1, *P*>0.11). However, test fish did ignore significantly more prey prior to capturing one following exposure to the bird-shaped model as compared to the fish-shaped one (χ^2=4.80, df=1, *P*<0.028).

There was no significant order of presentation effect (i.e., model presented on Day 1 or 2) on the distance juvenile salmon travelled to capture a prey item regardless of predator model used (4 models and 4 distance values for each model = 16 F values, all P values >0.05). Therefore, data for each predator model were pooled across day of presentation in subsequent analyses. There was no significant difference among the predator models in the distance (cm) test fish travelled to capture a prey item prior to exposure to a predation threat ($F_{3,52}$=0.60, *P*>0.62). However, exposure to both the kingfisher ($F_{3,39}$=11.69, *P*<0.0007) and bird-shaped model ($F_{3,30}$=10.80, *P*<0.0001) resulted in a significant decrease in the distance juvenile salmon travelled to capture a prey item (Fig. 2). This was true for the first ($F_{3,48}$=3.68, P<0.02), second ($F_{3,42}$=3.64, *P*<0.02) and third ($F_{3,43}$=3.87, *P*<0.02) prey item captured. The magnitude of this reduction in distance travelled did not differ between the first, second and third prey item captured following exposure to an aerial threat of predation (Fig. 2). In contrast, there was no significant reduction in the distance fish travelled to capture a prey item following exposure to either the brook trout ($F_{3,39}$=1.48, *P*>0.23) or fish-shaped models ($F_{3,25}$=1.01, P>0.41).

Discussion

Results from this study demonstrate that foraging juvenile Atlantic salmon show a different response to potential aerial and in-stream threats of predation. Salmon showed an escape response significantly more often, took significantly longer to resume foraging, and significantly reduced distance travelled to capture prey following exposure to the kingfisher model. In comparison, exposure to the brook trout model had little effect on juvenile salmon foraging activity.

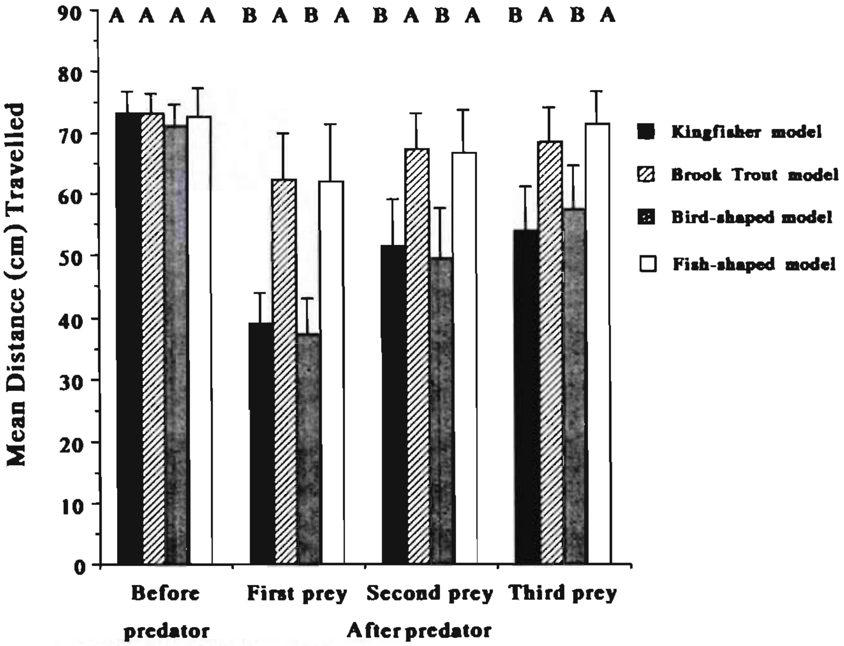

FIG. 2. Mean (+ 1 SE) distance (cm) juvenile salmon travelled to capture prey prior to, and to capture their first, second and third prey item following, exposure to either a kingfisher, brook trout, bird-shaped or fish-shaped model. Bars with the same letter above them are not significantly different.

Further, the observed predator avoidance behaviour exhibited by the salmon resulted in associated costs (i.e., number of prey ignored prior to resuming to forage), and a significantly greater cost was 'accepted' by the test fish following exposure to the kingfisher as compared to the brook trout model. Discrimination among and variation in the intensity of predator avoidance behaviour exhibited towards different predators has also been demonstrated in a number of other taxa (Coates 1980; Hirsch and Bolles 1980; Webb 1982; Magurran and Girling 1986; Foster and Ploch 1990). For example, Magnhagen and Forsgren (1991) found that sand goby (*Pomatoschistus minutus*) showed a more intense anti-predator response to an aerial (i.e., fish burrowed) versus a fish (i.e., fish formed groups) predator. They attributed this difference to the fact that bird predation represents an unpredictable threat to fish. A similar explanation could account for the observed difference in intensity of response shown by the juvenile Atlantic salmon towards the kingfisher and brook trout models in our study.

Predator discrimination by prey appears to be primarily based on visual cues provided by the predator (e.g., shape, colour, movement, etc.) (Karplus et al. 1982; Magurran and Girling 1986; Helfman 1989; Smith and Smith 1989), although other cues are also used (e.g., Magurran 1989). Usually, the approach of an unfamiliar or predator-like object will elicit predator avoidance behaviour in prey. However, prey have been shown to discriminate between such objects and actual predators with respect to the intensity of their avoidance response (Coates 1980; Magurran and Girling 1986). In the present study, although exposure to an overhead disturbance in the form of a bird-shaped model resulted in an anti-predator response (i.e., tendency to show an escape response, delayed foraging, and prey ignored), this was significantly lower in intensity than that shown towards the kingfisher model. A similar pattern in level of intensity of the anti-predator response was also observed with respect to exposure to a fish-shaped versus the brook trout model. These results suggest that juvenile Atlantic salmon are able to discriminate between a potential threat of predation and a predator-like disturbance on the basis of visual cues provided by the 'threatening' object. Given that both the bird-shaped and fish-shaped models were coloured to match a kingfisher and brook trout, respectively, discrimination by the salmon would appear to have been based on the absence of certain features (e.g., laterally extended wings, fins and head) on the predator-like models. Variation in the intensity of avoidance behaviour based on the absence or presence of specific features on the 'potential predator' has also been shown in other taxa (Karplus et al. 1982; Webb 1982; Magurran and Girling 1986).

Overall, the intensity of response to an in-stream threat of predation by test fish in this study was low. For example, juvenile Atlantic salmon showed a similar response to presentation of the brook trout and bird-shaped models, and virtually no response to a fish-shaped model. This weak response to an in-stream predator suggests that fish predation may not be very important in this population of juvenile Atlantic salmon. Such an interpretation of our results appears to be supported by the results of field studies, where brook trout was not found to be a major predator of juvenile Atlantic salmon (Gibson 1973). These field observations also provide another possible explanation for the significant difference observed in the response of test fish to the brook trout versus kingfisher model discussed earlier. If, as suggested, brook trout do not represent a major threat of predation, and given that salmon could monitor the approach and activity of the brook trout model, the lower intensity response shown towards this model could be viewed as appropriate.

In contrast to our results, foraging juvenile Atlantic salmon from a Scottish population (Metcalfe et al. 1987; Huntingford et al. 1988), and juvenile Pacific coho salmon (*Oncorhynchus kisutch*) (Dill and Fraser 1984), showed a strong anti-predator response to a model brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), respectively. However, both brown and rainbow trout are known to be predators of young Atlantic and Pacific salmon in these particular populations. Therefore, given the demonstrated ability of juvenile Atlantic salmon to discriminate between 'predators' in our study, might we have observed a higher intensity response to an in-stream threat of predation if we had presented the test fish with either a brown or rainbow trout model? In their study with deer mice (*Peromyscus maniculatus*), Hirsch and Bolles (1980) found that mice which had been raised in the laboratory nevertheless responded differentially to predators and non-predators if these were from the same natural habitat as the mice. In contrast, these same mice responded to both predators and non-predators from a different habitat in the same way as they did to non-predators from their own habitat. Based on their results, Hirsch and Bolles concluded that there was some innate capacity in the mice to recognize and respond appropriately to their natural predators. Similar innate/genetic 'programs' for predator/conspecific recognition have been suggested from the results of a number of other studies with a wide variety of taxa (Seghers 1974; Curio 1975; Owings and Coss 1977; Brown and Colgan 1986). Results from these studies also suggest that a 'predator blindness' (Curio 1975) may exist in naive prey towards predators not typically found in their habitat. Most Atlantic salmon rivers in eastern Canada and the United States historically have been, and remain so today, salmon-brook trout systems. This being the case, the significant difference in response to an aerial versus an in-stream threat of predation demonstrated by juvenile Atlantic salmon in this study may reflect the outcome of the selective forces acting on this population of salmon. If this were true, the use of a different species of fish predator would not be expected to alter the response of these fish to an in-stream predator. However, further work is needed to address the possibility of a genetic component in predator recognition in juvenile salmon.

Finally, if our results are representative of other Atlantic salmon populations in eastern North America, the absence of a strong anti-predator response to potential fish predation would suggest that extreme caution must be taken with respect to the introduction of exotic salmonids such as brown or rainbow trout into Atlantic salmon systems in this region, as these populations of salmon may not be adapted to adequately deal with this form of predation pressure. Losses to predation from in-stream sources following the introduction of such exotics, along with the negative effects that juveniles of these trout species can have on juvenile Atlantic salmon (Hearn and Kynard 1986; Kennedy and Strange 1986; Gibson 1988), together could prove devastating to the native stock of Atlantic salmon in that system. Results from our study would suggest that the predator-prey relationship between such exotics and native salmonids should be carefully examined before any introductions take place.

Acknowledgments

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In-Stream Movements of Young Atlantic Salmon (*Salmo salar*) During Winter and Early Spring[1]

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CUNJAK, R. A., AND R. G. RANDALL. 1993. In-stream movements of young Atlantic salmon (*Salmo salar*) during winter and early spring, p. 43–51. *In* R.J. Gibson and R.E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

A mark–recapture study of Atlantic salmon (*Salmo salar*) fry and parr was carried out in three streams of Atlantic Canada during 1–3 winters. In-stream movement was extensive between early-winter (November) and late-winter (immediately after ice-out, March/April) even at near freezing water temperatures and beneath ice cover. Percent recapture of the original marked population ranged between 2% and 30% by late winter and the number of unmarked fish (i.e., immigrants) was nearly always greater than residents. Emigration and/or mortality continued through late spring but was not as extensive as over winter. The low fidelity for riffle-run sites could not be explained solely by winter declines in density which varied between sites and years. Site fidelity was greatest in those streams where habitat conditions appeared most suitable for overwintering and was more pronounced among parr (ages 1 and 2) compared with fry. By late winter, mean fork length of resident salmon fry was consistently longer than that of immigrants each year and at all sites suggesting that site fidelity over the first winter was a function of fish size.

Une étude de marquage et recapture d'alevins et tacons de saumon atlantique (*Salmo salar*) a été réalisée dans trois cours d'eau de la région atlantique du Canada pendant un à trois hivers. Les déplacements dans le cours d'eau semblaient importants entre le début de l'hiver (novembre) et la fin de l'hiver (immédiatement après la débâcle, mars-avril), même à des températures proches du point de congélation et sous la couverture de glace. Le pourcentage de recapture de la population marquée était de l'ordre de 2 à 30 % à la fin de l'hiver, et le nombre de poissons non marqués (c.-à-d. immigrants) était presque toujours supérieur à celui des résidents. L'émigration et/ou la mortalité se maintenaient jusqu'à la fin du printemps, mais n'étaient pas aussi élevées que pendant l'hiver. Le faible degré de fidélité aux radiers ne pouvait pas s'expliquer simplement par les baisses hivernales de densité qui variaient d'un site à l'autre et d'une année à l'autre. La fidélité au site était au maximum dans les cours d'eau où l'habitat semblait le mieux convenir à l'hivernage, et était plus prononcée chez les tacons (âges 1 et 2) que chez les alevins. À la fin de l'hiver, la longueur à la fourche moyenne chez les alevins résidents était régulièrement supérieure à celle des immigrants chaque année et sur tous les sites, ce qui semble indiquer que la fidélité au site pendant le premier hiver est fonction de la taille du poisson.

Introduction

Movements of resident stream fishes, particularly salmonid species, have been studied in a variety of geographical locations (Gerking 1959; Saunders and Gee 1964; Edmundson et al. 1967; Bachman 1984; Dolloff 1987; Hesthagen 1988; Heggenes et al. 1991). The consensus from most studies was that the extent of movement was minimal (often <20 m), with the majority of the stream fishes being restricted to the immediate habitat-type(s) in which they were found during sampling. For example, de Leaniz (1989) found that long-term home areas were < 8 m^2 for 75% of Atlantic salmon parr in a Scottish stream which was monitored for 17 months.

During winter, especially in ice-covered streams, studies aimed at quantifying site fidelity and in-stream movements are rare (Chisholm et al. 1987) despite the fact that winter is a critical season in the life of young stream-resident fishes (Hunt 1969; Gardiner and Geddes 1980; Paragamian 1981; Myers et al. 1986). The primary objective of our research was to measure the site fidelity of stream-dwelling, young Atlantic salmon (*Salmo salar*) during winter. This was accomplished by sampling and marking immediately prior to freeze-up in early-winter (EW) with subsequent sampling and assessment of recaptures in the late winter (LW) just after ice break-up but prior to the spring thaw and spate. The frequency of occurrence of marked and unmarked individuals was assumed to represent site fidelity and the extent of immigration, respectively. The study was designed to sample only over that portion of the winter period when water temperatures had already declined below those stimulating the movement to wintering areas (2–7°C; Riddell and Leggett 1981; Hesthagen 1988) and adoption of a winter behaviour pattern (7–9°C; Rimmer et al. 1983; Cunjak 1988). As stream discharge (such as occurs in spring) is often correlated with stream fish movements (Huntsman 1945; Bagliniere 1976; Montgomery et al. 1983; Youngson et al. 1983), the effect of the spring spate (and rising

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water temperatures) was also investigated by sampling again in late spring (S) and the results compared with the winter movements.

A second objective of our study was to investigate whether or not winter movements within age-groups were size-related. This was accomplished by comparing the age and size structure of resident and immigrant salmon within the sites over winter.

As discussed by Cunjak and Power (1986), 'winter' is herein defined as that period following the autumn spawning of salmon (coincident with a steady decline in water temperature) and extending until a steady increase in water temperature, in spring, exceeds a diel mean of 4°C (usually accompanied by a major spate). Such a definition has more biological meaning than one based on calendar dates. During our study, therefore, 'winter' lasted from late October until mid-April.

Materials and Methods

Three stream sites, all riffle-run habitat types, were chosen to represent a variety of habitat conditions, regions and species combinations (Table 1). All three sites were typical of neighbouring stream reaches and each supported anadromous populations of Atlantic salmon, the most abundant salmonid species in these systems.

River Philip is located in western Nova Scotia and flows northeast into Northumberland Strait (45°50'N 65°40'W). The study site was located on one of the second order headwater tributaries, approximately 39 km upstream from the river mouth. It was sampled over three winters (1987/88, 1988/89, 1989/90). In 1987/88, initial sampling and marking took place in early November (EW) and subsequent sampling occurred only in late May (S) with no late winter (LW) sample. This was the only omission of the LW sampling date in the study. Catamaran Brook is a third order tributary of the Little Southwest Miramichi River in central New Brunswick (46°52.7'N, 66°06.0'W). A description of the basin and its biota was provided by Cunjak et al. (1990). The study site (located 8 km upstream from the river mouth) was sampled over two winters (1988/89 and 1989/90). The third study site was near the mouth of Betts Mill Brook (46°32.1'N, 66°11.4'W), a third order tributary of the main Southwest Miramichi River in New Brunswick. Betts Mill Brook was sampled over one winter only (1988/89) because early anchor-ice formation in the brook precluded initial sampling and marking in EW of 1989.

During electrofishing surveys to determine the abundance of fish, study sites were blocked off with barrier nets (0.6 cm mesh). Enclosed sections were electrofished from 3 to 4 times (except at River Philip during the May 1988 sampling (S) when only one electrofishing sweep was made) and all the captured fish were retained in screened cages until the survey was completed. At Betts Mill Brook, during the LW and S surveys, high water precluded the use of barrier nets. Instead, a 3 m apron-seine was used downstream of the electrofishing crew to capture fish before they were displaced from the study site by the strong water current. All salmonids were anesthetized (CO_2), measured (fork length [L], mm), weighed (wet weight [*W*], g), and marked using dye innoculation (Panjet, Alcian Blue) on the left caudal peduncle for EW samples. Additional marking of LW samples, on the right caudal peduncle, was performed in 1989/90 at Catamaran Brook and at River Philip. Marked fish were then released back into the study section and the barrier nets removed. During subsequent LW and S sampling, all fish were carefully examined and allocated to one of two groups: marked fish (i.e., residents) or unmarked fish (immigrants).

Densities of salmon were calculated using catch-depletion data and the removal method (Zippin 1956; Seber 1982) during the electrofishing surveys. This analysis yielded maximum-likelihood estimates of population size (*N*) and an estimate of the percentage of the population captured after the 3–4 sweeps. In no case were all the salmon within a site captured.

Site fidelity (*F*) was measured as the proportion of the original marked population of salmon (*M*) in EW

TABLE 1. Habitat descriptions of the study sites as measured during summer low flow conditions. S= salmon; T= brown trout; C= brook trout; L= juvenile lamprey; D= blacknose dace; P= sculpin. Substrate composition was defined as (BD) boulder/bedrock (>300 mm diam): (RU) rubble (150–300 mm): (C) cobble (50–150 mm): (GR)gravel (10–50 mm): (S)sand (0.1–10 mm): (SI) silt (<0.1 mm).

Study site	Area (m^2)	Mean depth (cm)	Mean water velocity (cm. s^{-1})	Substrate composition (%)	Fish spp. present
		±SD	±SD	BD RU C GR S SI	
River Philip	203	15.9±5.99	19.4±12.74	7-20-20-14-7-32	S,T,C,L
Catamaran Brook	228	13.0±8.49	18.9±17.51	21-12-26-36-5-0	S,C,D,P
Betts Mill Brook	274	24.6±15.65	43.8±30.37	5-23-17-20-22-13	S,C,P,L

which were subsequently recovered during the LW and S sampling surveys at each site (i.e., the number of recaptured (R) salmon):

(1) $F = [R/M]$

Where <95% of the estimated number of salmon at a site in EW were captured (N_0) for marking, it was necessary to account for these unmarked members (U) of the original population in calculating site fidelity in LW and S. In such cases, a corrected site fidelity (F_c) was applied :

(2) $F_c = [(U^*F)/N_1] + F$

where, $U = N_0 - M$; N_1 = estimated population size during the LW or S survey.

Growth information (mean lengths and weights) was recorded separately for the resident and immigrant groups of fish. Fulton's condition factor (K) was calculated for each fish, where $K = W/L^3 * 10^2$ (Ricker 1975).

Juvenile salmon were divided into two age-groups on the basis of length-frequency data. Age 0 salmon (designated as fry) could easily be distinguished because of their small size (Fig. 1) from older salmon (ages 1 and 2 and rarely, age 3 which were collectively designated as parr).

The null hypotheses that site fidelity was independent of season (i.e., LW or S) was tested using a Chi-square analysis of the frequency of immigrant (unmarked) versus resident (marked) salmon in a 2×2 contingency table. To adjust for continuity, the Yates correction was applied, as described in Zar (1974). That population structure was independent of season (or year) of sampling was tested by comparing the frequency of individuals in the two age groups (fry and parr) using 2×3 contingency tables. Differences in the mean size of salmon (i) in EW versus LW, and (ii) for resident versus immigrant salmon of each age group were tested using an independent t-test. Sample sizes were usually unequal and tests were based on separate variances for each group (Wilkinson 1990). Group means were considered significantly different at $P<0.05$. Where statistically significant differences in mean length between samples were found, the magnitude of the differences was expressed as relative growth (RG), where RG = $L_2 - L_1 / L_2 * 100$. L_1 and L_2 were the mean lengths of the two groups of fish being compared (EW and LW or resident and immigrant).

Results

Water temperatures during the period between fish-marking and subsequent sampling in late-winter remained near freezing (0.1–2.0°C) at all sites. Following the spring freshet, water temperatures measured at the study sites rose to between 5.0°C and 13.0°C by the time of the spring sampling .

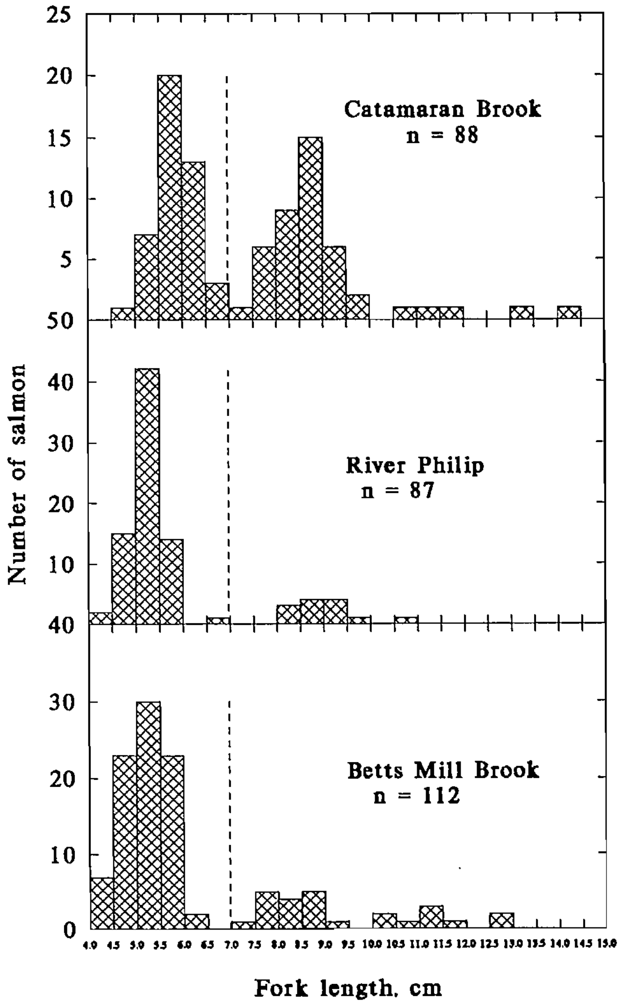

FIG. 1. Length-frequency distribution of young Atlantic salmon captured at Catamaran Brook, River Philip, and Betts Mill Brook in the early winter, 1988. The dashed vertical line at the 7.0 cm fork length position separates fry (age 0) from parr (≥ age 1); n = sample size.

Winter Movements

The results of the sampling immediately after ice-out (LW) in the streams suggest that site fidelity of young Atlantic salmon over winter was low. In Catamaran Brook and River Philip, the number of recaptured fish accounted for 19.1–30.3% of the original (EW) marked population (Table 2) in both 1989 and in 1990. At Betts Mill Brook, site fidelity by resident salmon was least, with only 1.8% (n=2) of the original (EW) population being recaptured in LW (Table 2).

Does low site fidelity over winter mean that in-stream movement was extensive at the near-freezing water temperatures or does the low percentage of recapture of salmon in LW reflect a high winter mortality? Two measures provide information on this question. Quantifying the frequency of occurrence of immigrant (unmarked) fish into the study sites provided a measure of in-stream movements. Second, a comparison of the changes in fish densities between

TABLE 2. Site fidelity of young Atlantic salmon (all ages pooled) over winter and spring during three years of study at River Philip, N.S., Catamaran Brook, N.B., and Betts Mill Brook, N.B. Data are expressed as numbers of salmon marked in early winter (EW), recaptured in late winter (LW) or spring (S), or captured without marks. Numbers in parentheses are percentages of the original (EW-marked) population. Asterisks denote adjusted percentages where <95% of the population was captured during sampling (see text for explanation).

	1987/1988		1988/1989			1989/1990		
	EW	S	EW	LW	S	EW	LW	S
River Philip								
marked/recaptured	70	10(14.3)	87	15(30.3)*	13(27.1)*	137	23(19.1)*	14(11.7)*
unmarked	—	67	—	80	62	—	76	59
Catamaran Brook								
marked/recaptured	—	—	88	18(20.5)	12(13.6)	53	9(20.0)*	7(15.8)*
unmarked	—	—	—	11	24	—	42	52
Betts Mill Brook								
marked/recaptured	—	—	110	2(1.8)	1(0.9)	—	—	—
unmarked	—	—	—	49	128	—	—	—

EW and LW provided an estimate of winter mortality assuming that habitat preferences did not vary over winter. This assumption appeared to be justified on the basis of water temperatures which were similarly low between the two dates.

On the question of in-stream movements, immigrants made up between 77% and 96% of the overwintering salmon population at Betts Mill Bk., R. Philip, and Catamaran Bk. (1989/90). The exception was Catamaran Bk. salmon in LW 1988/89 when immigrants accounted for only 38% of the salmon population. This exception was reflected in the significant ($P<0.05$) effect of season on site fidelity for that year; for the other locations and sampling dates, site fidelity of salmon was found to be independent of season ($P>0.400$).

Salmon density declined over winter in 4 of the 5 cases (Fig. 2). Site-specific declines in density were 35–40% at R. Philip, 54% at Betts Mill Bk., and 67% at Catamaran Bk (1988/89). The seasonal densities varied significantly ($P<0.005$) between years at Catamaran Brook. In 1989/90, the estimated density increase in LW likely reflects the poor electrofishing efficiency for this site and date (note the large SD, Fig. 2) as only 54% of the population was captured; when total catches per unit area were compared, the resultant densities indicated a slight decline over winter before returning to EW density levels by spring. At River Philip, estimated salmon densities were consistently highest among the sites (Fig. 2). The lowest estimated density of salmon was at Catamaran Brook in LW, 1989 (13.2 salmon/100 m^2), which was also the only occasion when residents outnumbered immigrants (see above).

By spring, the density of salmon remained low relative to the EW densities at River Philip (both years) and at Catamaran Brook (1988/89). At Betts Mill Brook, however, density of salmon in S rose markedly from that found in LW and was even higher than the EW density (Fig. 2). These data indicate an immigration into the site by non-residents as site fidelity by EW fish was lowest at Betts Mill Brook (Table 2).

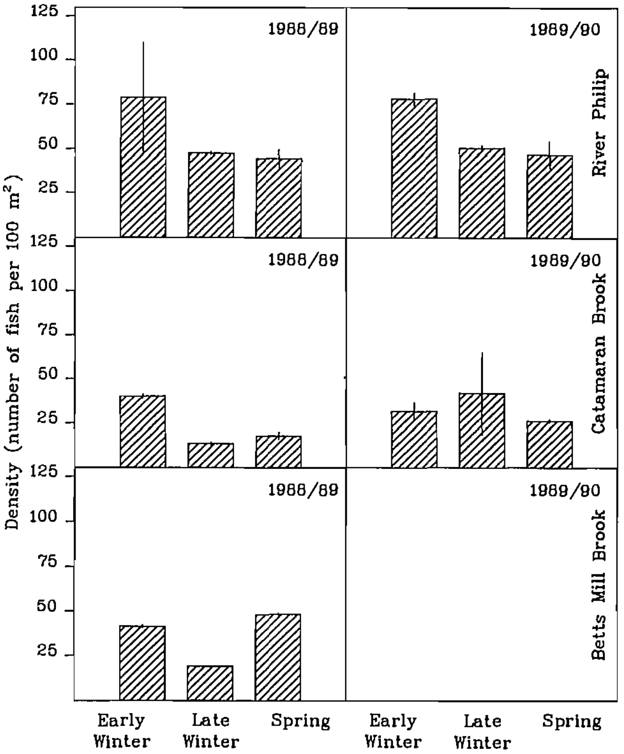

FIG. 2. Seasonal changes in the density (no. of fish per 100 m^2) of Atlantic salmon at the three study sites in 1988/89 and 1989/90. Vertical bars represent 1 SD.

Late-Winter to Spring Movement Patterns

Site fidelity through the LW to S period remained as low as was observed over winter, or continued to decline (Table 2). The percentage of salmon which remained in the study sites from EW to S ranged between 1 and 27% and varied between sites as well as between years.

The re-marking of fish in LW in 1990 permitted a more detailed assessment of the LW to S movements (Table 3). At Catamaran Brook and River Philip, Atlantic salmon marked in LW showed similarly low site fidelity (as was the case for EW-marked fish) with only 17–27% of the original marked populations being recaptured (Table 3). Some of the recaptures of EW salmon found in S were not present in the site during LW sampling. These 'homing' salmon represented 5.7% (n=3) and 8.0% (n=11) of the original EW marked population at Catamaran Brook and River Philip, respectively. Such data provide further evidence of significant in-stream movement over winter and suggest a return to the 'home' site, by spring, for a portion of the population which overwintered elsewhere in the stream.

A single electrofishing sweep of an equivalent stream area (and same habitat type) immediately above and below the River Philip site was made in the LW of 1989 and in the S of 1988 and 1989. This was done to assess if the small study area affected the frequency of occurrence of recaptured fish. However, only 4 marked salmon were recaptured which, on average, accounted for 1.6% of the original, marked population in EW.

Site Fidelity and Seasonal Movements as a Function of Age Group

Age 0 salmon (fry) were the most common age group found at the study sites, regardless of the date of sampling. From EW to LW, the proportion of fry increased at Catamaran Brook and at Betts Mill Brook (Fig. 3) although the population size of salmon declined steadily. This trend was particularly strong at Betts Mill Brook where a significant effect (P<0.001) of season on age group was found; the increase at Catamaran Brook was not significant (P>0.10). Salmon fry at River Philip (1988/89 and 1989/90) were similarly abundant (P>0.10) throughout the winter (84–85% of sample population, Fig. 3). By spring (S), population size of salmon increased at Catamaran Brook and Betts Mill Brook as did the percentage of fry (between 88 and 95%); at River Philip, however, the percentage of fry in the population declined or remained the same as in LW (54–84%) and population sizes declined (Fig. 3).

Salmon parr displayed greater site-fidelity (and/or survival) than fry in 10 of 12 comparisons (Table 4). Site fidelity was highest at Catamaran Brook where from 26–36% of the marked parr were subsequently recaptured in LW or S. That site fidelity was greater for salmon parr was particularly noteworthy in light of their low abundance relative to fry (Fig. 3). In 1989/90, when unique LW-marking was carried out to compare spring versus winter movement patterns, the recapture percentages were markedly similar between LW and S as they were over the winter (EW–LW), at both River Philip and Catamaran Brook (Table 4).

TABLE 3. Comparative site fidelity (%) of Atlantic salmon over the winter (November to March) and spring (March to May) for River Philip and Catamaran Brook in 1989/90. n refers to number of marked individuals at beginning of period.

	Winter		Spring	
Study site	n^a	Fidelity	n^b	Fidelity
Catamaran Brook	53	20.0	51	27.4
River Philip	137	19.1	99	17.0

[a] Number of salmon marked in early winter (November/December).

[b] Number of salmon marked in late winter (March).

Size Comparison of Resident and Immigrant Salmon

Resident salmon fry generally increased in length over the winter (Fig. 4) and the increase was significant (P<0.05) at River Philip (both years) and at Catamaran Brook in 1988/89. Condition factor of resident fry generally declined over winter but was significant only at River Philip in 1989/90. Resident yearling parr (only age 1 were sufficiently abundant for this analysis) showed no significant (P>0.200) differences in fork length (Fig. 4) or in condition factor over winter.

For salmon parr, both fork length (Fig. 4) and weight of residents were not significantlly different (P>0.05) from those of immigrants by LW. Condition factors of resident and immigrant salmon parr were also similar except at Catamaran Brook (1989/90) where condition of resident parr was significantly higher (P<0.05) than immigrants in LW.

Resident salmon fry were consistently longer than immigrant fry at all sampling sites in LW (Fig. 4) but the difference was significant (P< 0.05) only at

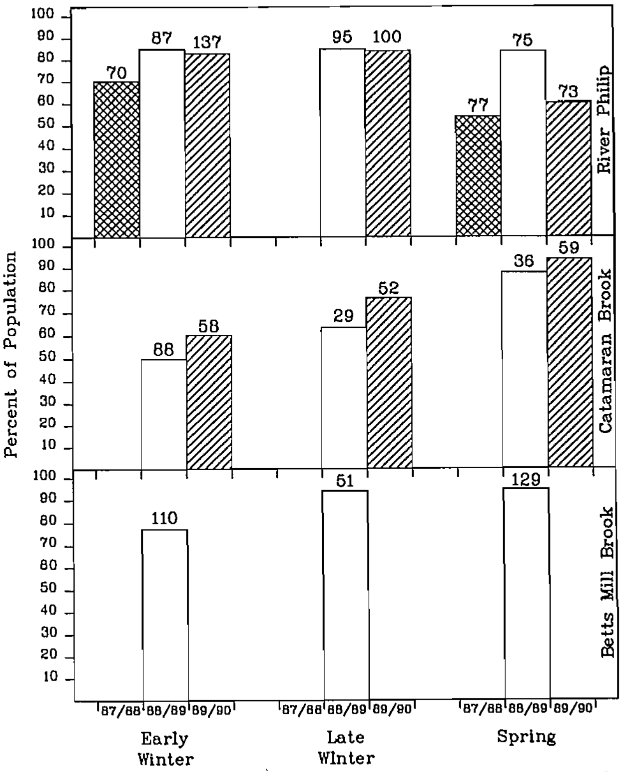

FIG. 3. Seasonal changes in the percent representation by fry (age 0) in the sampled population of Atlantic salmon, at three sites over three years. Numbers atop the bars refer to the total number of salmon (all ages) sampled on each date.

TABLE 4. Percent representation by salmon fry and yearling parr (age 1) as determined by recaptures of marked fish over winter and in spring from three (3) rivers. EW = early winter (November/December); LW = late winter (March/April); S = spring (May/June). Note: LW marking of fish was only done in 1989/90.

YEAR	LOCATION	Sample Interval EW ⟶ LW		EW ⟶ S		LW ⟶ S	
		Fry	Parr	Fry	Parr	Fry	Parr
1988/89	Bett Mill Brook	2.4	0	0	6.3	—	—
	Catamaran Brook	36.4	30.8	4.5	25.6	—	—
	River Philip	14.9	25.0	13.5	16.7	—	—
1989/90	Catamaran Brook	8.3	33.3	2.8	33.3	8.3	35.7
	River Philip	14.2	26.7	9.2	20.0	16.0	28.6

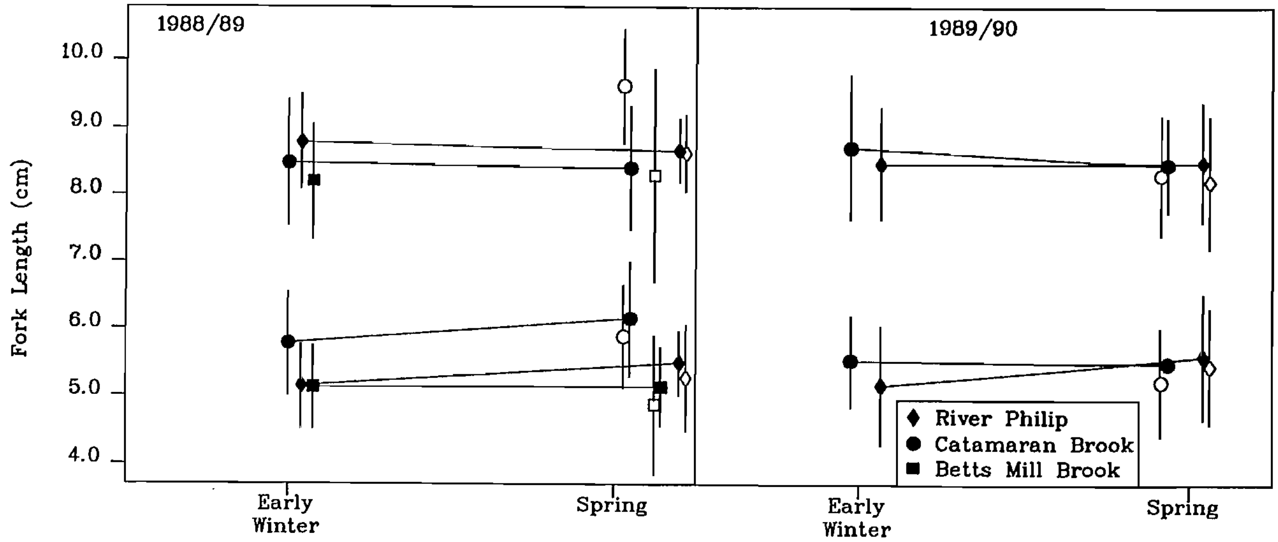

FIG. 4. Comparative changes in the mean fork length (± 1 SD) of resident (solid points) versus immigrant (open points) salmon fry and yearling (age 1) parr over two winters.

River Philip (1988/89). Weights and condition factor of fry were similar between the two groups with no case where resident fry were significantly different than immigrant fry.

Discussion

Juvenile Atlantic salmon exhibited significant in-stream movements during winter at the three rivers in eastern Canada which were monitored during this study. Even at near-freezing water temperatures and beneath an ice cover, the majority of juvenile salmon displayed little fidelity for the stream sites where they were originally captured in the early-winter. Instead, unmarked (migrant) salmon usually dominated the catches by late winter. This finding is in contrast to a previous study of site fidelity of Atlantic salmon fry and parr over winter. In Girnock Burn, Scotland, de Leaniz (1989) recaptured 71% of the original population of salmon parr within 20 m of the marking location after 17 months with fidelity being strongest in immature parr. Between August and December in the Waweig River, New Brunswick, Saunders and Gee (1962) recaptured 76% of marked parr from 2 to 123 days after release, nearly all of these being recaptured in the vicinity of original home sites. However, Saunders and Gee (1962) did note a scarcity of marked parr and fry in December (water temperature of 0.1°C) which they attributed to habitat shifts to wintering areas or to an emigration to spawning sites (by mature parr). Similarly, in an earlier study at Catamaran Brook during the ice-free season, Randall and Paim (1982) found that most salmon parr (> 80%) at two sites were residents from July to September, but the proportion of residents decreased to < 50% in October and November. Autumnal movements of parr in New Brunswick streams have been attributed to changes in microhabitat requirements, particularly substrate size, at the onset of winter (Rimmer et al. 1984) or to the higher energetic costs associated with overwintering in 'severe' stream environments. Our study documents that the in-stream movements of Atlantic salmon continue throughout the winter in ice-covered streams.

The winter movements of juvenile salmon were probably related to the severe winter conditions which affect riverine habitats in eastern Canada. We hypothesize that because of prolonged periods of near-freezing temperatures (0.1°C), together with the dynamic ice conditions and fluctuating water levels, in-stream movements by salmon to suitable wintering habitats are common in Canadian streams and that these movements continue throughout the winter months. Such heightened winter activity by young salmonids in ice-covered streams may be an ecologically adaptive response to unstable stream conditions (Reimers 1963; Cunjak and Power 1986). The fact that water temperatures in the Girnock Burn study cited above (de Leaniz 1989) were somewhat higher than in our study streams might explain the higher site fidelity of salmon observed there in winter. Even at Girnock Burn, however, continuous winter movements by a small number of parr did occur, possibly reflecting the unstable nature of the stream during winter (Youngson et al. 1983).

Habitat shifts by young salmon in autumn are associated with a decline in water temperature below 8–10°C (Gibson 1978; Rimmer et al. 1983). However, our study suggests that subsequent movements and/or habitat shifts are occurring at water temperatures near freezing as well. It is likely that ice, in its various forms (surface, anchor, frazil) and associated phenomena (e.g., freezing, damming, habitat exclusion), may act as another stimulus for inducing fish movement. A recent observation lends support to such a theory. Underwater observations in a small P.E.I. stream during the morning after the first anchor ice formation of the winter yielded no evidence of resident brook trout which were abundant throughout the section the previous week; the few remaining trout were found in the shallow stream edges beneath limited surface ice cover where anchor ice does not form. Chisholm et al. (1987), using radio telemetry to monitor brook trout movement in ice-covered Wyoming streams, speculated that ice may be important in affecting fish habitat and the behaviour of fish, especially where stream channels were shallow and conducive to ice formation.

Site fidelity in the three study streams was more pronounced for parr than fry, particularly by the spring when 6–33% of the early-winter marked parr were recaptured compared with 0–13% for fry. A similar trend was noted by Saunders and Gee (1964) who found site fidelity of parr to be approximately twice that of fry. During their early winter sampling, Saunders and Gee (1964) noted a shift by fry into winter habitats which were deeper and had larger substrates than the summer habitat. In our study, the greater tendency of fry to move over the winter compared with parr was further demonstrated by the increasing proportions of fry found at the sites by late winter. Possibly, movements of juvenile salmon were density-dependent as fry were significantly more abundant than parr at all sites. Chapman (1966) and Bjornn (1971) suggested that winter movements of salmonids in West Coast streams may be density-dependent, especially where suitable winter habitat was limited.

Availability of suitable winter habitat may also explain the observed variability in site fidelity among the study streams. Stream salmonids minimize energy expenditure in winter by selecting suitable microhabitats which offer protection from strong current velocities and ice, and from freezing (Cunjak and Power 1986). Where the requisite seasonal microhabitat requirements can be met in the immediate stream habitat/reach, in-stream movement may be minimal (e.g. Rimmer et al. 1983, 1984; Dolloff 1987).

Movement beneath suitably-sized rock shelters is the common tactic employed by young salmon for overwintering (Rimmer et al. 1983; Cunjak 1988). Where shelters are limited or where access beneath rocks is impeded by imbedded fine particles (sands, silts), movement to other stream habitats may be necessary (Hillman et al. 1987). At Betts Mill Brook, mean water velocity was greatest and large substrates (boulder/rubble) were scarcer than at other sites. Many of the cobbles at this site were imbedded by sand and silt, more so than at the other two sites. Anchor ice was also more commonly observed at this site, perhaps because of the more open canopy which is conducive to anchor ice formation. Lack of suitable winter habitat may account for the extremely low site fidelity (<2%) of Atlantic salmon at the Betts Mill site.

Inter-specific competition may be another factor which reduced habitat availability and thereby, site fidelity, of wintering salmon. Slimy sculpin (*Cottus cognatus*) was the most abundant fish species found at the Betts Mill site with an estimated early winter density of 95.1 individuals per 100 m^2, more than twice that of the salmon. As these sculpins also reside beneath stones, competition with salmon for this space is a possibility. Chapman (1966) considered space to be the primary density regulator of stream fish in winter and Cunjak (1986) speculated on the role of competition for similar winter microhabitats for a variety of stream species.

Increases in salmon density at Betts Mill Brook from LW to S (i.e., a return to EW densities) suggests that this site may serve strictly as rearing habitat during the ice-free season. Electrofishing surveys over the past decade confirmed that the site was important as a rearing habitat for fry in summer (R.G. Randall, pers. obs.). The seasonal importance of specific stream habitats for different life-stages underlines the importance of year-round investigations of fish behaviour and habitat use for fisheries management.

The different winter conditions experienced during 1988/89 and 1989/90 might explain the variability in site fidelity at Catamaran Brook, particularly in 1988/89 when density declined most (67%) and immigration was least (38% of the sampled LW population). Discharge data from nearby hydrometric gauging stations (Environment Canada 1987–1990) indicated that water levels during the winter of 1988/89 were extremely low in the Catamaran Brook area with only slight increases in discharge relative to the other years and sites under study. Low water levels, in combination with the high number of days with freezing conditions and ice accumulation compared with the River Philip area (where environmental conditions are less severe), may have limited in-stream movements within the shallow Catamaran Brook site.

The decline in density over winter might be used as an indicator of winter mortality, in which case mortality at our sites ranged between 35 and 67%. Incorporating the data of those 'surviving' salmon which homed to the stream sites in S (i.e., 6–8% of the EW population) and those salmon recaptured in adjacent stream reaches (i.e., ~2%), estimated winter mortality would be between 25 and 57%. However, this assumes that migrating salmon to and from the study sites had equal survival over winter and that all stream habitats were equally suitable for overwintering. Such assumptions are probably invalid. Future studies aimed at discerning winter mortality and emigration need to select larger stream sections which include a variety of available habitat-types (e.g. riffles, flats, pools). The stream sites in our study were exclusively shallow riffle-runs and may not be the preferred habitats of all age-classes and for all winter conditions.

Although we were unable to precisely differentiate the contributions of mortality and movements over winter, a number of factors indicate that winter movements (emigration) from the sites can account for much of the observed low site fidelity. The high proportion of immigrant salmon in LW and the occurrence of EW-marked fish in S (but not found in LW) provide strong evidence of significant in-stream movement. That density had increased again to EW levels after a LW decline (e.g., Betts Mill) suggested that movement, rather than mortality, was the explanation and that salmon were perhaps displaying seasonal habitat preferences. Because no growth is assumed over winter (Gardiner and Geddes 1980) and as resident fry generally increased in length over winter, the results suggest an emigration by smaller-sized residents or a size-selective mortality phenomenon. The consistently smaller size of immigrant fry at the sites compared with residents, in both years, supports the explanation of emigration.

Site fidelity by salmon during spring, as in the winter, was low. Judging from the density changes between LW and S, mortality would seem to have less of an impact over the spring period compared with over winter. Rather, in-stream movements likely accounted for most of the observed changes in site fidelity at this time of year. Spring discharge is known to displace stream fishes (Huntsman 1945; Montgomery et al. 1983) although such displacements can also result in mortalities (Harvey 1987).

The consistently larger size of resident salmon fry compared with immigrant fry has interesting implications. Body size of juvenile salmonids has a positive effect during competitive interactions and the establishment of dominant status (Jenkins 1969; Wankowski and Thorpe 1979) and also for increasing winter survival (Lindroth 1965; Hunt 1969). Further, experiments with salmonids have shown that individuals which are introduced into a new location experience higher mortality rates than resident fish (Noakes 1978) perhaps because of risks associated with moving to unfamiliar areas (Dolloff 1987). Investigations to compare mortality rates of winter resident and immigrant fry may provide valuable information on the population dynamics of fry during winter.

In summarizing information on in-stream movements of juvenile salmonids, Elliott (1986) noted that there are three distinct periods of spatial movements: 1. downstream movements of newly emerged fry from redds; 2. movements of fry in autumn to deeper pools for overwintering; 3. increased mobility of fish before and during the smolt emigration. All migrations are related to maximizing food supply or are a response to adverse conditions. As noted above, similar patterns of movement of Atlantic salmon fry and parr have been observed during the ice-free seasons (Meister 1962; Thorpe and Morgan 1978; Riddell and Leggett 1981; Randall 1982; Buck and Youngson 1982; Youngson et al. 1983; Chadwick and Leger 1986; and Cunjak et al. 1989). In addition to these generalizations about the movements of salmonids, we emphasize that in-stream movements during winter are also significant in ice-covered streams. Without question, further detailed observations and experimentation are needed to understand the effects of winter conditions, particularly ice, on the habitat and the survival of juvenile Atantic salmon in eastern Canada.

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Relative Habitat Use, and Inter-Specific and Intra-Specific Competition of Brook Trout (*Salvelinus fontinalis*) and Juvenile Atlantic Salmon (*Salmo salar*) in Some Newfoundland Rivers

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Relative habitat utilization by brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) in three third-order rivers in southeastern Newfoundland was quantified. Brook trout populations were measured over seven years in various habitats in one river, two years before and five years after salmon were introduced. Changes in brook trout populations were compared with two nearby rivers, one of which has a natural run of salmon, and another where brook trout was the only salmonid. In riffle areas salmon biomass was relatively greater than trout biomass, and total salmonid biomass was greater than when only trout were present. Trout had the relatively higher biomass in pools and in a pond habitat, and the total salmonid biomass did not show a significant increase in these habitats. The results indicate that in riffles young salmon could use part of the habitat little used by trout, but that in slower water trout could use most of the habitat that salmon also used. Diving observations showed that smaller fish of both species occupied shallower water than larger fish. In all types of habitat salmon held position closer to the substrate than trout. Without salmon, brook trout, older than underyearlings, occupied faster water velocities than where salmon were present. A negative density-growth relationship of young salmon was apparent in riffle habitats.

Nous avons quantifié l'utilisation relative de l'habitat par l'ombe de fontaine (*Salvelinus fontinalis*) et les juvéniles de saumon atlantique (*Salmo salar*) dans trois rivières de troisième ordre du sud-est de Terre-Neuve. Les populations d'omble de fontaine ont été mesurées pendant sept ans dans divers habitats d'un cours d'eau, deux ans avant et cinq ans après l'introduction des saumons. On a comparé les changements dans les populations d'ombles de fontaine avec celles de deux cours d'eau proches, dont l'un possède une remontre naturelle de saumon et l'autre comptait l'omble de fontaine comme seule salmonidé. Dans les zones de radiers, la biomasse de saumon était relativement supérieure à celle de l'omble, et la biomasse totale de salmonidés était plus élevée que lorsque seul l'omble était présent. L'omble présentait une biomasse relativement plus élevée dans les fosses et dans un habitat d'étang, et la biomasse totale de salmonidés ne montrait pas d'augmentation significative dans ces habitats. Les résultats indiquent que, dans les radiers, les jeunes saumons peuvent utiliser une partie de l'habitat qui est peu exploitée par l'omble, mais que dans les eaux plus lentes l'omble peut utiliser la plus grande partie de l'habitat qui est aussi occupé par le saumon. Des observations faites en plongée ont montré que les petits poissons des deux espèces occupaient des eaux moins profondes que les poissons de grande taille. Dans tous les types d'habitat, le saumon se tenait en position plus proche du substrat que l'omble. En l'absence de saumon, les ombles de fontaine âgés d'un an et plus occupaient des eaux au courant plus rapide que lorsque le saumon était présent. Une relation négative densité-croissance chez les jeunes saumons était apparente dans les habitats de radiers.

Introduction

Brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) are co-occurring indigenous salmonids in many seaboard rivers of eastern Canada, where frequently they are the dominant fish species. A number of studies suggest that brook trout occupy relatively slower water habitat than young salmon and have greater preference for shade and submerged cover than salmon, so that in general juvenile Atlantic salmon are considered primarily as riffle or fast water dwellers and brook trout as typical inhabitants of pools or stream margins (Keenleyside 1962; Gibson 1966). Although selective segregation may account for many of the differences found in habitats occupied, a wide range of types of stream habitat is used by both species. Furthermore, food and feeding behaviour of both species are similar (Gibson et al. 1984; Thonney and Gibson 1989). Inter-specific competition, therefore, might be expected when resources become limiting, and interactive segregation (Nilsson 1978) between the two species has been demonstrated in a Québec river (Gibson 1973).

Long-term studies by the Canadian Department of Fisheries and Oceans in experimental rivers in southeastern Newfoundland have provided the opportunity for the first time to examine interactions between the two species in a river when Atlantic salmon were introduced where previously brook trout had been the only salmonid present. Questions addressed in the present paper were: what was the relative distribution of the two species in different types of habitat;

were there changes in habitat use and biomass of brook trout after introduction of Atlantic salmon; and what intra-specific effects could be seen?

Further reference to Atlantic salmon will be simply as 'salmon', or with certain juvenile fluvial stages as 'underyearling' salmon, or '0+', 'salmon parr' (older than 0+), or 'smolt' (the stage where migration to sea can occur). Similarly, brook trout will be referred to as 'trout', except where there could be confusion with other trout species.

Experimental sites

Research was conducted in three third order rivers in southeastern Newfoundland: Freshwater River at Cape Race (46°38'50"N; 53°05'40"W); Drook River near Portugal Cove South (46°40'16"N; 53°14'35"W); and Northeast Brook at Trepassey (46°46'0"N; 53°21'10"W). Basin areas of the three systems are respectively, (km^2), 16.83, 13.21, and 21.23. The three systems are within 21km of each other, and are similar in that each rises in boglands and small shallow lakes, 122 to 152m above sea level, and flows from 6 to 7 km to the sea (Fig. 1). The area is in the 'eastern hyper-oceanic barrens' ecoregion (Damman 1983), characterized by maritime barrens with patches of stunted boreal forest. Winters are relatively mild, and summers are cool with frequent sea fog (Banfield 1983). Mean annual air temperature (Cape Race) is 4.3°C, and mean annual precipitation 1379 mm (Environment Canada 1982). Bedrock geology is of sandstone, olive to green argillite, siltstone, shale and silicified tuff (King 1988).

Northeast Trepassey Brook has a natural run of anadromous salmon. In all years, runs were high and egg deposition rates for riverine habitat were over $5 \cdot m^{-2}$ (M.F. O'Connell, DFO, St. John's, NF, pers. comm.). Salmon are naturally absent in the other two rivers. Drook River drains to sea through a barrier beach, and Freshwater River has a precipitous falls at its mouth, both being barriers to immigration by salmon. However, for experimental reasons, adult salmon were introduced to Freshwater River annually from 1985 to 1990 (Table 1), providing potential egg deposition in fluvial habitat ranging from approximately $2.0–6.0 \cdot m^{-2}$. Brook trout and threespine stickleback, *Gasterosteus aculeatus* L., are present in all three rivers. Eel, *Anguilla rostrata* (Le Sueur), are abundant in Northeast Trepassey Brook, rare in Drook River, and absent in Freshwater River. Limited angling for trout occurs in Drook River, but is prohibited in the other two. None has habitations or other developments upstream from a road crossing the lower end of each river.

Materials and Methods

Sites for population estimates were selected within a river system in representative reaches. Within each reach, stations were stratified by types of habitat (Frissell et al. 1986). Stations representing each type of habitat were therefore selected within each 'stream order' (*sensu*, Horton 1945, modified by Strahler 1957). If a habitat change occurred in a segment, such as a pond or lake, stations were selected both above and below such standing water. We attempted to make replicate stations of habitat types within each reach under study, but resources dictated that we selected single habitat types within some reaches and not all tributaries were sampled. Stations were sampled during the summer between the second week of July and mid-August, after the main growing period.

General types of habitat were taken from Allen (1951). Terminology varies with different authors, e.g., riffle and stickle, flat and glide, run and rapids; but habitats can be classified into the following major groups, which all overlap, and of course merge into one another: cascade; riffle; run; flat; pool; lake. Velocities and depths delineating these are given in Table 2. 'Cascade' was not sampled in the present study. Our basic strata therefore were the various tributaries, and within each, where possible, the following types of habitat: riffle; flat; pool; run. This classification was not used in derivation of multiple linear regression models, for which values of the measured habitat variables were used.

All of a habitat type was included within a station. A station was barricaded off with upstream and downstream nets of 0.6 cm square mesh, with the downstream net being installed first. Workers kept well away from the sides of the river bounding the station until both nets were in place, only entering the water to place the nets. Rubble and boulders for securing the bottom of the barrier nets were taken from outside the station, which was disturbed as little as possible, since the same stations were sampled in following years. Population estimates in shallow fast water areas (riffles) were made using an electro-fisher by the depletion method (Zippin 1958), with at least four sweeps, moving in an upstream direction. In deeper, slower waters the electro-fisher was not always effective, in which case fish were caught also by beach seine, and by fyke nets in lakes, and estimates made by the mark and recapture Petersen method or, in larger lakes, by the multiple mark and recapture, or Schnabel, method (Ricker 1975). All fish were anesthetized with CO_2, by dissolving an Alka Seltzer tablet in a few litres of water, and measured by fork length (total length for sticklebacks and eels), and placed in a recovery cage before release. Marked fish had two fins clipped. About 10 salmonids from each year-class were killed for age, weight, and sex analyses, which included staging of maturity (Kesteven 1960). These samples were measured fresh the same evening. Condition factors (K) were calculated from the expression, $K = W \cdot 10^2 \cdot FL^{-3}$, where W=weight (g) and FL= forklength (cm). The individual weights of all fish collected were calculated from the mean condition factor for each particular length. Ages were assigned to length frequency histograms after scale reading and verification of size groups. In autumn sampling mature male parr could be identified by their girth and frequently by release of sperm with pressure, and these were identified separately for condition factor and weight, since they were relatively heavier than immature male and female parr.

Habitat variables that were measured are shown in Table 3. Length and width to the nearest 0.1 m were measured with a tape measure. Two lengths (left and right banks) were taken if there were some curvature and usually three width measurements were made (both wet widths and bank to bank). At least five depths were taken at equidistant points across three transects, divided by $n+1$ to account for 0 depth at the edges. Mean water velocity (0.6 depth) was measured at 1/4, 1/2, and 3/4 the distance across. Until 1989, water velocities were measured with a Hiroi acoustic current meter, and, from this time also and at most sites, with a model 201D Marsh McBirney current meter. The maximum depth was recorded with a metre-stick (or a plumb line in lakes). A proxy variable was used as an indicator for range of discharge. For this we used either ice scour height, or height of flood debris, since some rivers lack an ice scour mark. Where both variables were measured, they were highly correlated ($r^2=0.9$). We visually estimated the

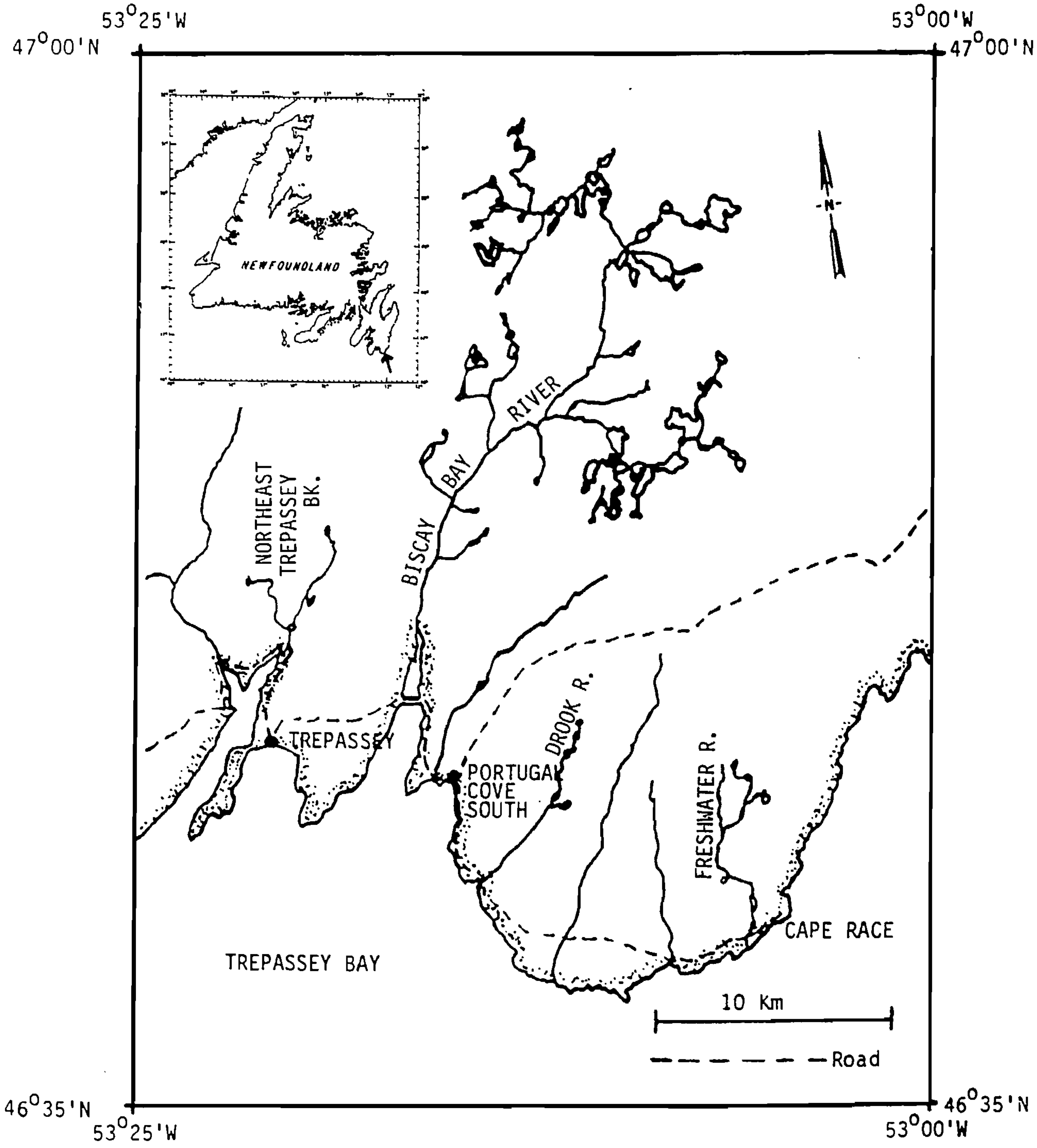

FIG. 1. The location of the experimental rivers in southeastern Newfoundland.

TABLE 1. Numbers of adult salmon introduced to Freshwater River, and the ages of emigrating smolts.

Year	#Adult salmon introduced	Proportion female	Potential egg deposition[a]	Smolts			
				2+	3+	4+	5+
1985	239	0.74[b]	612 818				
1986	111	0.68[b]	261 290				
1987	121	0.74	310 007				
1988	120	0.69	285 911	270			
1989	74	0.76	194 628	381	3211		
1990	110	0.78	296 927	0	1256	891	
1991	0	—	0	38	322	354	123

[a] Mean weight of female grilse, 1.68 kg; fecundity, 2 066 eggs/kg (M. F. O'Connell and J. B. Dempson 1991). Mean no. eggs retained, ~ 10.2/female grilse.

[b] Derived from emigrating kelts, the others were sexed before introduction.

TABLE 2. The major types of habitat recorded. Habitat types were taken from Allen (1951).

Pools:	Of two groups: pools, with current of less than 38 cm· s^{-1}, and depth 46 cm to 68 cm; and, *deep pools*, with current less than 38 cm· s^{-1}, and depth over 68 cm. The flow is smooth apart from a small turbulent area at the head of some pools.
Flats:	Current under 38 cm· s^{-1}, mean depth under 46 cm. Flats are sections of relatively shallow water, but with a smooth surface.
Runs:	Current over 38 cm· s^{-1}, mean depth over 23 cm. The flow is usually turbulent. In such places the stream is usually of less than average width.
Riffles:	Current over 38 cm· s^{-1}, mean depth under 23 cm. These are shallow water with a rapid current and usually a broken flow.
Cascades:	These are rapids in which a steep gradient, combined with a bed of stones or rocks large in proportion to the size of the stream, produces a very irregular rapid flow, often with some white water.

proportion of each type of substrate category (Bain et al. 1985). Extent of the three types of cover (instream, overhanging and canopy) was estimated visually. Riparian vegetation type was also recorded, identified to common names in the field book, but coded as to % of coniferous, deciduous, and open with grasses and shrubs. Conductivity and temperature were also recorded.

Biomass and densities for 1984 were correlated with various attributes by a stepwise regression technique, at 17 stations in Northeast Trepassey Brook, 13 stations in Freshwater River, and 13 stations in Drook River. Variables were entered in the regression model only if the variable was significant at $P<0.15$. Variables were selected by a forward stepwise procedure with deletion (Neter and Wasserman 1974).

Diving observations were made in riffle, flat, and pool type habitats at standard stations during the summer (on dates varying from June 27–August 31), from 1985 to 1990, in each river. Physical characteristics of the sites are given in Table 4. A total of 577 fish observations were made. A wet-suit, mask and snorkel were worn, and the observer quietly entered the water downstream of each station. Each fish was observed from a distance of 1 m or greater. If this was a regular holding station, as judged from feeding behaviour or defense of the area, the location of the fish was marked with a small lead weight having a numbered and colored tag. Species, estimated size of the fish, and estimated distance above the bottom, as well as location, tag color and number, were recorded underwater on a sketch of the station in a waterproof notebook. Since distances are distorted underwater, some practice with observing measures of length underwater on a metre-stick was done at the start of each dive. Estimated sizes of fish were later designated to age classes, as found in the population studies. Underyearlings (0+) of each species were easily assigned to their age class. Small salmon parr (<10 cm F.L.) and large salmon parr (>10 cm F.L.) were easily distinguished and were equivalent to 1+, and 2+ and older fish, respectively. However, we had less confidence in assigning ages to the trout, which were therefore all designated as 1+ if older than 0+. After observations were made, depths were measured with a metre-stick, and water velocities measured at the recorded location of each fish (nose velocity) with a Beauvert type 81S micro water velocity meter. Habitat of each station was measured as described

TABLE 3. The habitat variables measured for derivation of the stepwise multiple regression equations (Adapted from Platts et al. 1983 and Bain et al. 1985).

Mean (wet) stream width (MWIDTH) (m) — usually at three locations in the station $\times n^{-1}$.

Mean depth (MDEPTH) (cm) — usually five equidistant locations at the same transects as the width measurements $x\ (n+1)^{-1}$.

Mean water velocity (VEL) ($m \cdot s^{-1}$) — measured at 0.6 of the depth at 1/4, 1/2, and 3/4 of the width, at the same locations as the width and depth measurements.

Maximum flood height (MAXFLDH) (cm) — experimental rivers, or ice scour height (m), Highlands River — an indicator of range of discharge.

Maximum depth (MAXDEPTH) (cm).

Substrate rating (SUB) — Each proportion of substrate type is multiplied by the rating, and the results summed for a general substrate rating.

irregular or convoluted bedrock	7
very large boulders, 2.5–4 m	6
large boulders, 1.5–2 m	
medium boulders, 0.55–1 m	
small boulders, 25.5–50 cm	
rubble, 15.5–25 cm	5
cobble, 6.5–15 cm	4
pebble, 1.65–6 cm	3
gravel, 2.5–16 mm	2
sand, 0.1–2 mm	1
silt, 0.004–0.06 mm	
clay, ≤0.0039 mm	
organic detritus	
flat bedrock	

Chemical — Nitrate nitrogen; total alkalinity; total phosphorous; total dissolved solids; Hydrogen ion; total hardness; calcium; chloride; sulphate; colour (one colour unit represents the colour of $1 mg \cdot L^{-1}$ platinum solution when viewed in a depth of 200 mm).

Instream cover (INSTRCOV) (%) — undercut banks, tree debris, aquatic plants, etc.

Overhanging cover (OVCOV) (%) — structures up to about 1 m above the surface and providing shade, such as alder bushes, etc.

Canopy cover (CANCOV) (%) — shade over the stream provided by trees.

Specific conductivity (SPCOND) ($\mu s \cdot cm^{-1}$).

TABLE 4. Mean width, depth, and mid-depth water velocity characteristics, at diving stations. n = number of observations. Standard deviations are in parenthesis.

	Riffle	Flat	Pool
Mean width (m)	5.9 (3.26)	5.3 (1.64)	6.6 (2.99)
Mean depth (cm)	18.8 (4.80)	22.9 (8.50)	41.4 (7.85)
Mean velocity ($cm \cdot s^{-1}$)	40.7 (14.28)	17.4 (8.37)	14.3 (9.53)
n	19	25	19

previously. Analyses of distribution were performed with rank transformation, since residual plots were not normal (Conover and Iman 1981).

Morphometric measurements, made by caliper of preserved samples of salmon and trout from Northeast Trepassey Brook (upper jaw and pectoral fin length), were regressed against standard length (S.L.). These measurements were chosen to examine differences in two of the major characteristics which probably serve in separation of feeding and habitat niches of the two species.

Results

Biomass and densities related to habitat variables

Analyses of relationships for the three rivers in 1984 are given in Tables 5 and 6. Both model and adjusted r^2 values are presented. The adjusted r^2 provides a modified measure which recognizes the number of independent variables in the model (Neter and Wasserman 1974). The results indicate total salmon biomass was greatest and that large parr were most abundant over a coarse substrate (Table 5). Densities of 2+ parr had a negative relationship with mean water velocity, related probably to their more frequent occurrence in deeper water than small parr (Fig. 2). The negative relationship of salmon biomass with conductivity and nitrates was unexpected, but there may have been confounding factors related to preferred habitat and distance from the sea, with the latter influencing deposition of salts such as sodium chloride which has little effect on production, but the effects of nutrients being overridden by other factors.

Trout biomass showed a negative relationship with maximum flood height and therefore a positive

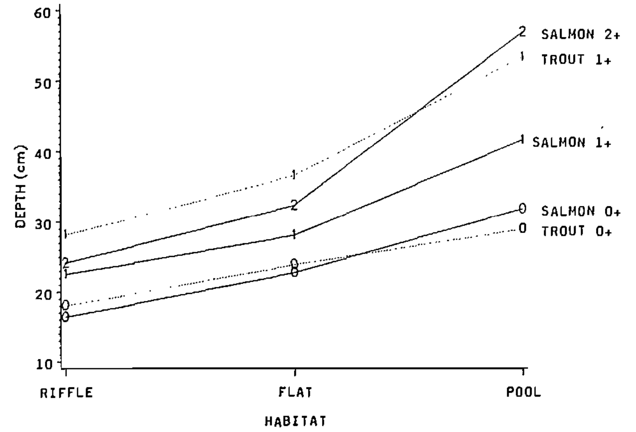

FIG. 2. Mean depths of Atlantic salmon and brook trout in three types of habitat, as observed by diving. There was no significant difference in depth distribution between species (P>0.05), but a highly significant difference between underyearling fish (<6 cm) and small (>6 cm <10 cm) salmon (P>F=0.0001), and between small salmon and larger salmon (>10 cm) and trout (>6 cm), (P>F=0.001). Underyearlings are designated as 0+, small salmon were likely to be yearlings, or 1+, and large salmon were designated as 2+, but some may have been older. All trout older than 0+ were designated as 1+.

relationship with stable water flows (Tables 5 and 6). In Northeast Brook there was a negative relationship of biomass with water velocity (Table 5), but not in rivers without the presence of salmon, where in fact there was a positive relationship (Table 6).

Diving Observations

Distributions as seen by diving are shown in Fig. 2, 3, and 4. As might be expected, fish were seen in deeper water as depth increased (P>F=0.0001). However, in each type of habitat, older and larger fish occupied deeper water than younger fish (Fig. 2). We could not reject the hypothesis that there was no difference in depths selected by species (P>0.05), but there was a significant difference between depths selected by the underyearlings of salmon and trout and the older fish (P>F=0.0001), and small (1+) salmon were seen in shallower water than 1+ and older trout, or 2+ and older salmon (P>F=0.0001). Greatest difference seen between trout and salmon was in height held above the substrate (P>F=0.0001). As shown in Fig. 3, in all types of habitat, salmon were closer to the substrate than trout. Underyearling salmon remained in contact with, or close to, the substrate in the three types of habitat, but parr in slower water were frequently above the substrate. The difference was significant between mean height held by 1+ and larger salmon versus that of underyearlings (P>F=0.002).

Nose velocity measurements of fish older than 0+ (>6 cm) are shown in Fig. 4. The underyearling fish are omitted for clarity. The velocities for underyearling salmon were (cm·s^{-1}) (S.E. in brackets): riffle 12.8 (3.68); flat 12.7 (1.78); pool 6.1 (0.96). Since underyearling salmon usually apply themselves directly to the substrate, actual nose velocities were probably lower, a possibility also with salmon parr that were in contact with the bottom. The velocities for 0+ (underyearling) brook trout were (cm·s^{-1}): riffle, 7.1 (6.0); flat 5.5 (0.89); pool 7.0 (0.80). Large parr in pools tended to select faster flows than small parr (P>F=0.0019). Trout older than fry in the river without salmon (Drook) were seen in faster flows than in the rivers with salmon (Northeast Trepassey all years, and Freshwater after 1986); (P>F=0.0001).

Relative Changes in Biomass and Densities

The relative biomass of salmon and trout in the three rivers in 1984 before introduction of salmon to Freshwater River is shown in Table 7. Trout biomass was lowest in Northeast Trepassey Brook, which had high densities of salmon, and the relative proportion of trout biomass in pools: riffles (2.4) was greater than in the other two rivers (1.6 in Drook and 0.7 in Freshwater), indicating relatively greater use of pools by trout in Northeast Trepassey Brook.

Changes in densities and biomass of salmon and trout at representative stations in Freshwater River are shown in Fig. 5–10, and of trout at two riffle stations in Drook River in Fig. 11. Salmon fry first emerged in Freshwater River in 1986, so the three normally dominant age classes (0+, 1+ and 2+) were not all present until 1988. Generally the majority of smolts emigrated at 3+ in late spring, after maximum water temperatures reached 9°C (Table 1). Some 1+ and 2+ parr also emigrate with the smolt run (Gibson et al. 1990). However, some parr older than 2+ remained in the river (Fig. 9–10).

The biomass and densities of salmon were highest in the riffle habitats (Fig. 5 and 9a). Yearling parr were abundant in 1987, and mean biomass in the riffle stations was 3.1g·m^{-2}. In 1988, with an additional year class, the mean riffle biomass was 4.7 g·m^{-2}. The higher densities of 0+ in 1986, 1+ in 1987 and 2+ in 1988 were a consequence of the relatively high egg deposition in 1985 (Table 1). In flats, mean salmon biomass rose to 2.5 g·m^{-2} (Fig. 6), and in pools approximately to 2.0 g·m^{-2} (Fig. 7). Trout biomass at sites in riffles and flats decreased from when first measured in 1984, and remained lower, but cannot be related to the presence of salmon, at least until 1986, when salmon underyearlings were present. Trout biomass in the riffles remained lower than that of salmon after salmon parr were present, but total salmonid biomass in 1987, 1988, and 1989 (5.1, 6.3 and 5.7 g·m^{-2}) was similar to or higher than the highest trout biomass measured (5.4 g·m^{-2} in 1984). In other types of habitat, relative salmon biomass was lower, and total salmonid biomass did not increase over that with just trout alone. Biomass of salmon was lowest in the pond habitat (Fig. 8). In contrast to riffle and flat habitats, in the pool habitats 2+ and 3+ trout were most numerous in the 1986 sampling period (Fig. 10a), with a consequently higher biomass in that year (Fig. 7). Both salmon and trout were least numerous in the pond habitat (Fig. 10b).

TABLE 5. Stepwise multiple regression equations for salmon and trout in Northeast Trepassey Brook, 1984.

	Model[b]	Model r^2	Adjusted r^2
Salmon Variable[a]			
Biomass	= 6.95 − 0.19 (SPCOND) +1.02 (SUB) − 0.05 (NITR)	0.69	0.615
Density 0+	= −21.24 + 0.46 (MAXFLDH)	0.36	0.32
Density 1+	= −68.31 + 1.28 (CHL)	0.45	0.42
Density 2+	= −12.54 + 0.75 (SUB) − 37.54 (VEL) − 0.18 (INSTRCOV)	0.61	0.52
Trout Variable[a]			
Biomass	= 5.6 − 0.03 (MAXFLDH) − 0.02 (MWIDTH) − 4.06 (VEL)	0.76	0.70
Density 0+	No variables selected by stepwise regression		
Density 1+	= 66.16 − 8.99 (VEL) − 0.32 (TPH) − 0.67 (CHL)	0.62	0.53
Density 2+	= 3.32 − 0.07 (MWIDTH) + 0.16 (TPH) − 0.04 (MAXFLDH)	0.65	0.57
Density 3+	= 10.52 + 0.004 (MAXFLDH) − 0.02 (INSTRCOV) − 0.27 (SPCOND)	0.85	0.81

[a] Dependent variables: Total salmon or trout biomass (g·m^{-2})
Densities of 0+, 1+, 2+ and 3+ salmon or trout (·100 m^{-2})
[b] Independent variables: SPCOND = specific conductivity (µs·cm^{-1}); SUB = substrate rating; NITR = nitrates (mg·L^{-1}); MAXFLDH = maximum flood height (cm); CHL = chloride (mg·L^{-1}); VEL = mean water velocity (m·s^{-1}); INSTRCOV = instream cover (%); MWIDTH = mean stream width (m); TPH = total phosphorus (mg·L^{-1}).

TABLE 6. Stepwise multiple regression equations for brook trout in Freshwater and Drook rivers in 1984.

Trout Variable[a]	Model[b]	Model r^2	Adjusted r^2
Biomass	= 1.87 + 0.08 (CALC) + 10.82 (VEL) − 0.09 (MAXFLDH)	0.87	0.84
Density 0+	= −44.24 + 1.14 (SPCOND) + 0.26 (TPH) − 0.17 (MAXFLDH)	0.60	0.52
Density 1+	= 1.08 + 0.20 (CALC)	0.39	0.35
Density 2+	= 9.70 + 1.26 (NITR) + 0.17 (MAXDEPTH)	0.40	0.33
Density 3+	= 16.40 + 0.30 (INSTRCOV) − 0.25 (TPH)	0.59	0.54

[a] Dependent variables: Total trout biomass (g·m^{-2})
Densities of 0+, 1+, 2+ and 3+ trout (·100 m^{-2})
[b] Independent variables: CALC = calcium (mg·L^{-1}); SPCOND = specific conductivity (µs·cm^{-1}); SUB = substrate rating; NITR = nitrates (mg·L^{-1}); MAXFLDH = maximum flood height (cm);
CHL = chloride (mg·L^{-1}); VEL = mean water velocity (m·s^{-1}); INSTRCOV = instream cover (%); MWIDTH = mean stream width (m); TPH = total phosphorus (mg·L^{-1}).

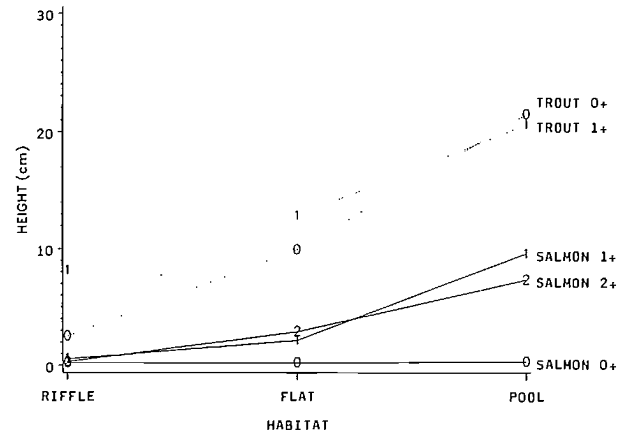

FIG. 3. Relative mean heights above the substrate observed of salmon and brook trout during the summer in three types of habitat. Differences between species were highly significant ($P>F=0.0001$). There was no significant difference between heights of underyearling trout and older trout ($P>0.05$), but mean height of underyearling salmon was significantly different from that of both small salmon and large salmon ($P>F=0.002$).

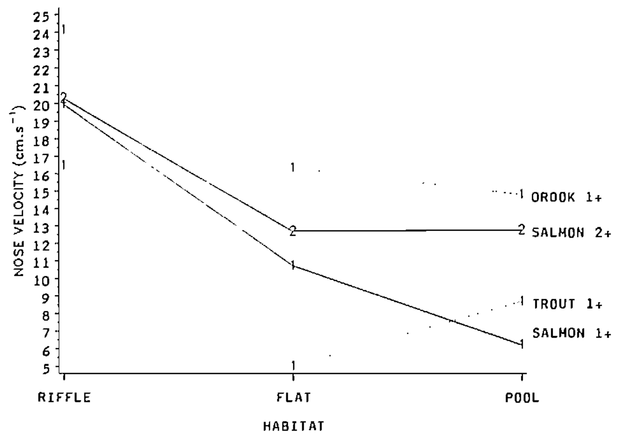

FIG. 4. Mean nose velocities of salmon and trout older than 0+ (>6 cm), as observed by diving, in three types of habitat. Trout were seen in faster water in Drook River (Drook 1+), where there were no salmon, than when coexisting with salmon (Trout 1+), $P>F=0.0001$.

TABLE 7. Mean biomass ($g{\cdot}m^{-2}$) of salmonids[a] at stations in the Experimental Rivers, Trepassey Bay, Newfoundland, in 1984.

	Northeast Brook		Drook River	Freshwater River
Habitat type	Salmon	Trout	Trout	Trout
Riffles	4.06	0.83	11.30	4.95
	(1.42)	(1.26)	(5.04)	(2.57)
n	11		6	6
Run	2.36	0.30	—	—
	(1.87)	(0.00)		
n	1			
Flats	2.78	0.97	19.42	6.32
	(1.24)	(0.49)	(4.34)	(1.94)
n	4		4	4
Pools	3.25	2.00	17.93	3.47
	(0.38)	(2.00)	(7.12)	(1.10)
n	3		3	3
Lake	0.47	0.42	1.96	1.39
	(0.20)	(0.25)	(0.45)	(0.39)
n	1		1	1
Mean area of stations other than lakes (m²)	198		130	195
(Range)	(65–463)		(52–353)	(63–565)
Area of lake (ha)	7.27		2.73	1.1
Mean depth of lake (m)	3.80		0.62	0.34

[a]Standard deviations in parentheses or 95% C.L. where only one station.

Biomass of brook trout in the two riffle habitats in Drook River was higher in 1984 (18.4 $g{\cdot}m^{-2}$) than in the 6 following years (Fig. 11). The biomass in 1984 was augmented by relatively more 3+ trout ($35.8{\cdot}100\text{-}m^{-2}$, 16.0 $g{\cdot}m^{-2}$) than were found in following years. The biomass dropped to 9.5 $g{\cdot}m^{-2}$ in 1985 and fluctuated in following years between 9.6 and 13.8 $g{\cdot}m^{-2}$. In the riffle habitats of Freshwater River, the trout biomass similarly dropped in 1985, from 5.4 to 2.7 $g{\cdot}m^{-2}$. However, the high biomass of trout in riffles of Freshwater River in 1984, and to a lesser extent in 1985 (Fig. 5), was a consequence of high densities of 2+ trout in riffles in those years (Fig. 9a).

Intra-specific competition

A negative correlation of mean weight with density was apparent with yearling salmon in riffle habitats (Fig. 12). No significant relationship was found for other types of habitat, partly due to few samples and low densities. Density dependent size relationships were not found with trout.

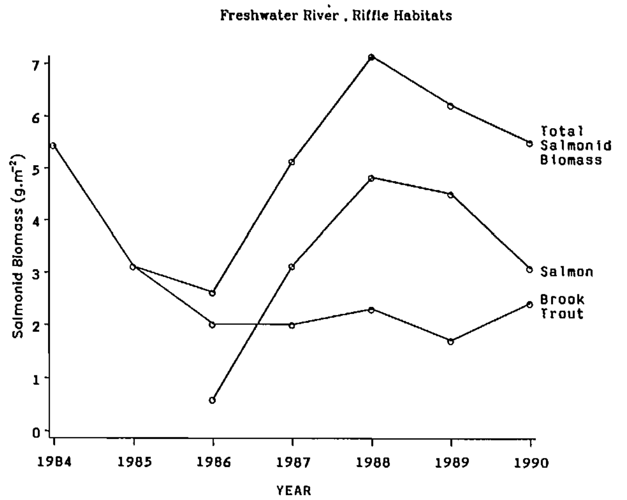

FIG. 5. Changes of salmonid biomass at three "riffle" habitat stations in Freshwater River from 1984 to 1990. Adult salmon were introduced in 1985.

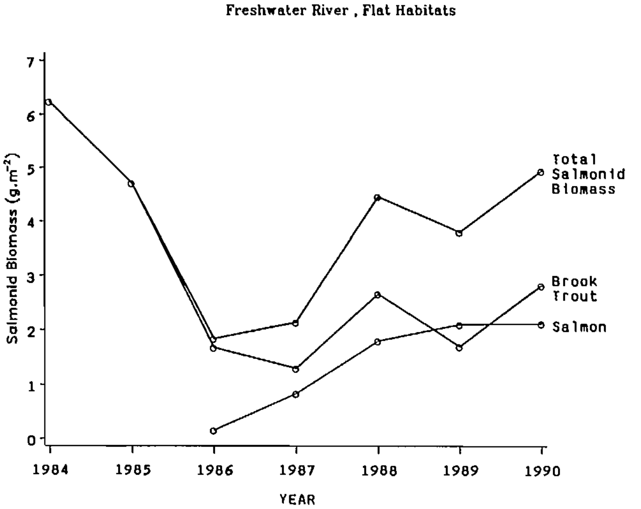

FIG. 6. Changes of salmonid biomass in two "flat" habitats of Freshwater River.

The maturation of male parr is a function of growth (reviewed in Thorpe 1986) and therefore can be related to density-dependent effects. No male parr less than 7 cm in fork length was found to be maturing, similar to findings of Myers et al. (1986). Relative sizes and proportions of maturing parr of sampled male salmon from fluvial habitats are shown in Fig. 13. Data from 1987 to 1990 are presented, since yearling parr were present in Freshwater River only after 1986. Five age classes were present in 1990, although in Northeast Trepassey Brook all five year-classes were present at high densities in all four years, most probably accounting for the more linear relationship of age and size between years in this river ($r^2 = 1.00$, compared with $r^2 = 0.97$ in Freshwater River). The proportion of maturing male parr increased with size and was greater in Freshwater River where mean size of parr was larger than in Northeast Trepassey Brook (Fork length Freshwater River = 2.8 Age + 4.7; Fork length N.E. Trepassey Brook = 2.1 Age + 4.9).

Morphometric measurements

The ratio of upper jaw: standard length of salmon was 1:8.82 (SD 0.81, n=38), with a range in SL of 29.5–112.0 mm, and with trout was 1:6.73 (SD 0.54, n = 29), with a range of SL of 27.8–142.0 mm. Relative regressions were: salmon, Y(jaw) = 0.11 (SL) + 13.56 ($r^2 = 0.95$); trout, Y(jaw) = 0.15 (SL) − 38.19 ($r^2 = 0.95$). The slopes were significantly different ($P < 0.01$).

The ratio of pectoral fin length: SL was 1:4.31 (SD 0.36) for salmon, and 1:5.36 (SD 0.44) for trout. Regressions were: salmon, Y(fin) = 0.20(SL) + 187.52 ($r^2 = 0.95$); trout, Y(fin) = 0.18(SL) + 83.16 ($r^2 = 0.96$). The slopes were significantly different ($P < 0.01$).

Discussion

In the model for salmon in Northeast Trepassey Brook, densities of 2+ and total biomass of parr had positive relationships with coarse substrate. Similarly, in a fourth order river in southwestern Newfoundland, the Highlands River, total density of parr and salmon biomass were found to have positive relationships with substrate rating (Gibson et al. 1987). That study also showed negative relationships with mean width and % overhanging cover.

Similarly, in the river systems of the present study multiple linear regression equations have identified a negative relationship of stream width with biomass and densities of salmonids (Gibson 1990; Gibson et al. 1990).

Water chemistry variables also control stream production (Binns and Eiserman 1979; Johnston et al. 1990). However, in the present study levels of nutrients were low and their effects were overridden by other factors. Hynes (1969) remarked that in shallow clear streams, where nutrients are limiting, nitrates and phosphates could increase production of fish. This was illustrated in enriched streams in St. John's, Newfoundland, where salmonid production was very much higher than measured elsewhere on the island of Newfoundland (Gibson and Haedrich 1988).

In the present study, brook trout biomass had a negative relationship to maximum flood height, indicating that habitats with the more stable stream flows had higher production. In the Highlands River, where a more diverse range of habitats could be sampled, findings were similar. Brook trout biomass had negative relationships with ice scour height, mean width and mean water velocity, and positive relationships with % overhanging cover and mean depth.

A major difference compared to salmon was that densities of trout in the Highlands River had a negative relationship with coarseness of substrate. Biomass of trout, which better represents larger fish, was greater in smaller streams with stable discharge, in lower velocities and deeper water (i.e., pools), and where there was overhanging cover. The regression models of these

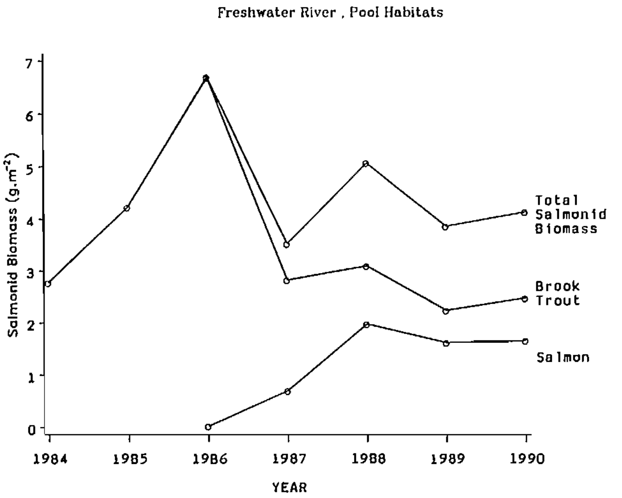

FIG. 7. Changes of salmonid biomass in two "pool" habitats of Freshwater River.

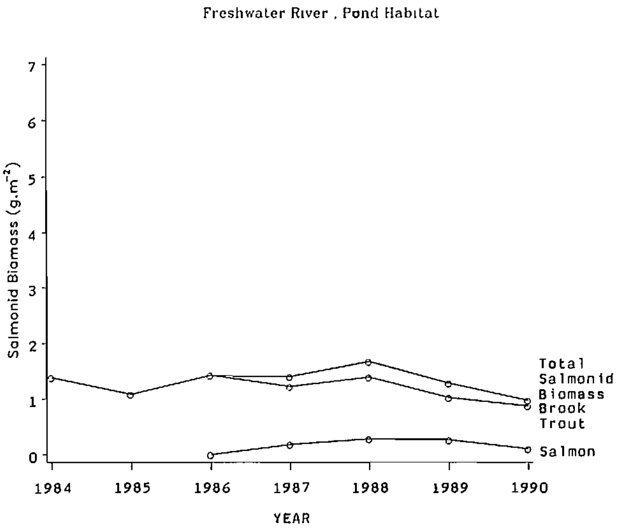

FIG. 8. Changes of salmonid biomass in a "pond" (shallow lake) habitat of Freshwater River.

studies affirm qualitative descriptions, but better quantify habitat segregation of the two species.

The increase in salmonid biomass in riffle stations, after the introduction of salmon, and the relatively greater proportion of salmon to trout in this habitat suggest that salmonid carrying capacity was higher with the two species present and that salmon were able to exploit parts of the habitat not previously used by trout. Similar conclusions have been made with salmon and brown trout, *Salmo trutta* (Kennedy and Strange 1980; Gibson and Haedrich 1988). Total salmonid biomass did not increase in slower and deeper types of habitat, and relative proportion of trout was higher, suggesting that in these latter areas competition by salmon was less severe on trout than in the riffle habitats, although salmon may have been exploiting part of the habitat previously used by the trout.

Although in both Drook River and Freshwater River highest trout biomass in riffle habitats was in 1984, and decreased in both rivers afterwards, trout biomass in pool and pond habitats of Freshwater River fluctuated less. Real changes in the population may therefore be masked by different responses in preferred and less preferred habitats, and are also affected by water conditions and season.

Factors other than climatic ones may affect population cycles in the two rivers, so that Drook River trout populations may not act as a valid control for trout in Freshwater River. Without more information on factors affecting cycles in the trout populations, it is not possible to say with certainty that trout populations had been affected in Freshwater River by invasion of juvenile salmon after 1986. The differences in trout biomass between rivers suggest that differences in physical features between rivers control trout densities to a large extent. For example, Drook River has abundant submerged cover in the form of the moss *Fontinalis* sp. and has many spring seepages in the lower section of the river, so that the water temperature can actually be cooler nearer the mouth than nearer the headwaters, features differing somewhat from the other two rivers and which may partially account for the high trout biomass in this river.

Our findings are somewhat different from conclusions of a study in the Matamek River, Québec (Gibson 1973). In that study, both salmonid species were abundant in rapids and riffles in the early part of the season when food was abundant, but, later in the summer when food was sparser, trout were found mainly in deeper water, whilst salmon remained abundant in shallower, faster water. At a similar station without salmon, trout remained abundant in fast water habitats throughout the summer. Since in the present study measurements were made in late summer, and not through the season, it is possible similar movements occurred and that there was interactive segregation leading to the observed distributions.

In the Matamek River there was evidence that trout had a negative effect on growth of large salmon parr in a pool-type habitat (Gibson and Dickson 1984). Also Ryan (1993) has shown in two Newfoundland lakes an inverse correlation between brook trout and salmon densities, although the direction and mechanism of possible competition were unknown. In comparison, brown trout, a close ecological equivalent of brook trout, can influence the distribution of young salmon, which occupy slower flowing areas in the absence of brown trout (Heggenes 1991). In European rivers brown trout are considered severe competitors of young salmon (Kennedy and Strange 1986a).

Salmon may have negative effects on numbers of yearling trout in some habitats (Gibson and Myers 1986), thus possibly reducing recruitment to older groups. It is possible that higher densities of salmon in Freshwater River, similar to those occurring in Northeast Trepassey Brook, could have measurable negative effects on the trout, as is suggested by the relatively low trout numbers in Northeast Trepassey Brook. Further manipulations of the stocks are required to test this hypothesis. Since the trout in Freshwater River had

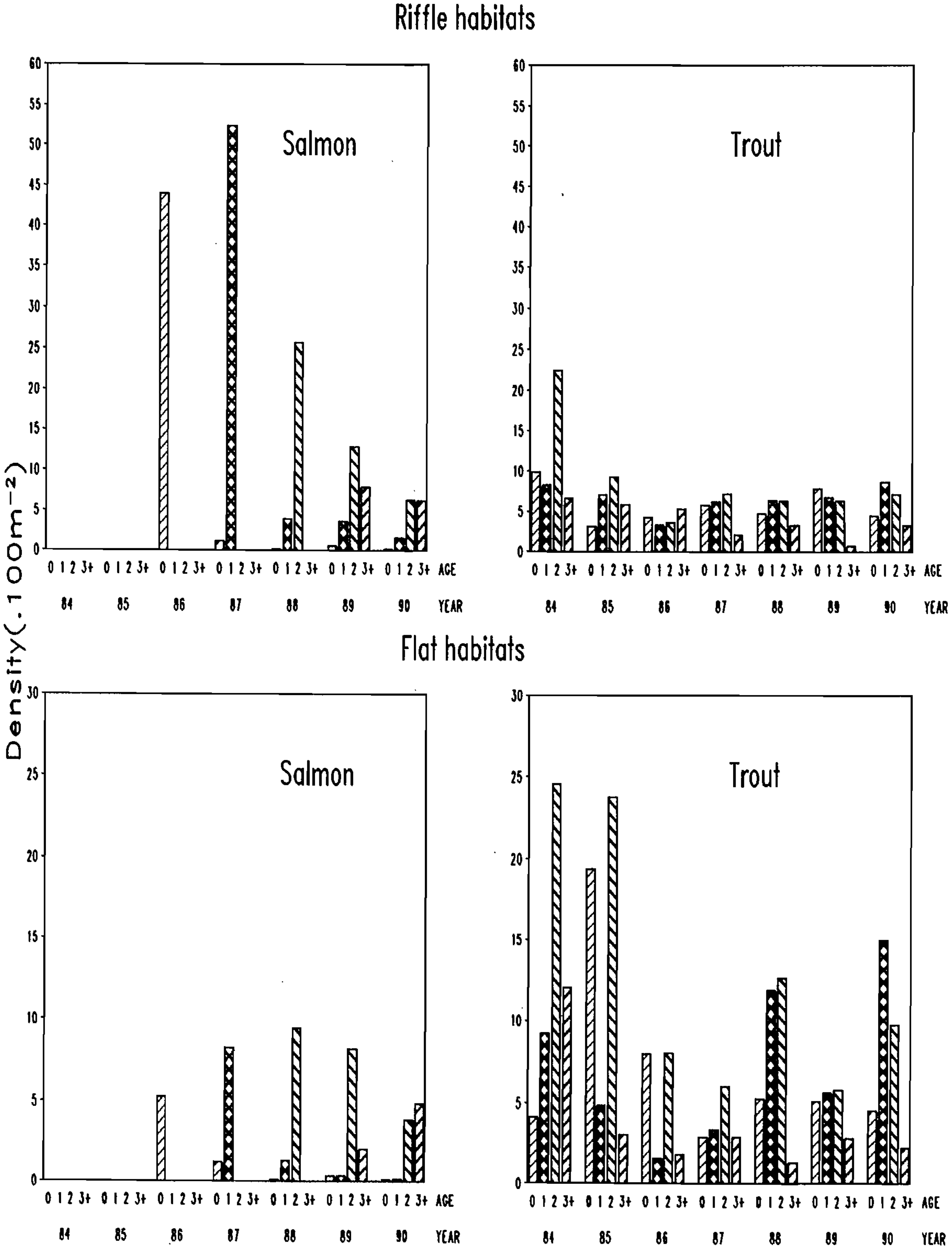

FIG. 9. Changes in densities of salmonids in: (a) the riffle habitats of Freshwater River; and (b) flat habitats of Freshwater.

been living allopatrically without competition from salmon, there is also the possibility that there may be genetic differences in behaviour and morphology between trout in Northeast Trepassey Brook and Freshwater River, affecting relative competition with salmon. However, although possible character differences in the trout stocks should be examined, the ecological compatibility seen suggests that, if there were differences, they were small.

The underwater observations illustrate the effects of types of habitat on holding stations of salmon and trout. Selected depths, velocities, and distance above the substrate, varied with type of habitat, suggesting that relating distribution to a single variable may not always be meaningful. In addition, distributions are strongly influenced by inter-specific competition and by predation (reviewed in Gibson 1988).

Underwater observations have been used to derive 'habitat suitability curves' for young salmon (DeGraff and Bain 1986; Morantz et al. 1987). Those authors found that 'nose velocity' was the principal variable influencing positions of juvenile salmon. Our findings suggest that, although such curves may be useful for describing optimum dimensions of a variable for some specific life history stage under certain conditions, their applications are too simplistic and do not account for interactions among variables. Habitat suitability curves however derived from macrohabitat density evaluations may have wider applicability (Scruton and Gibson 1993).

Smaller fish occupied shallower water than larger fish (Fig. 2). This relative distribution has been related in other fish species to greater risk for larger fish by avian predation in shallow water and to greater competitive and predatory pressure by larger fish on smaller fish in deeper water (Power 1987; Power et al. 1990;

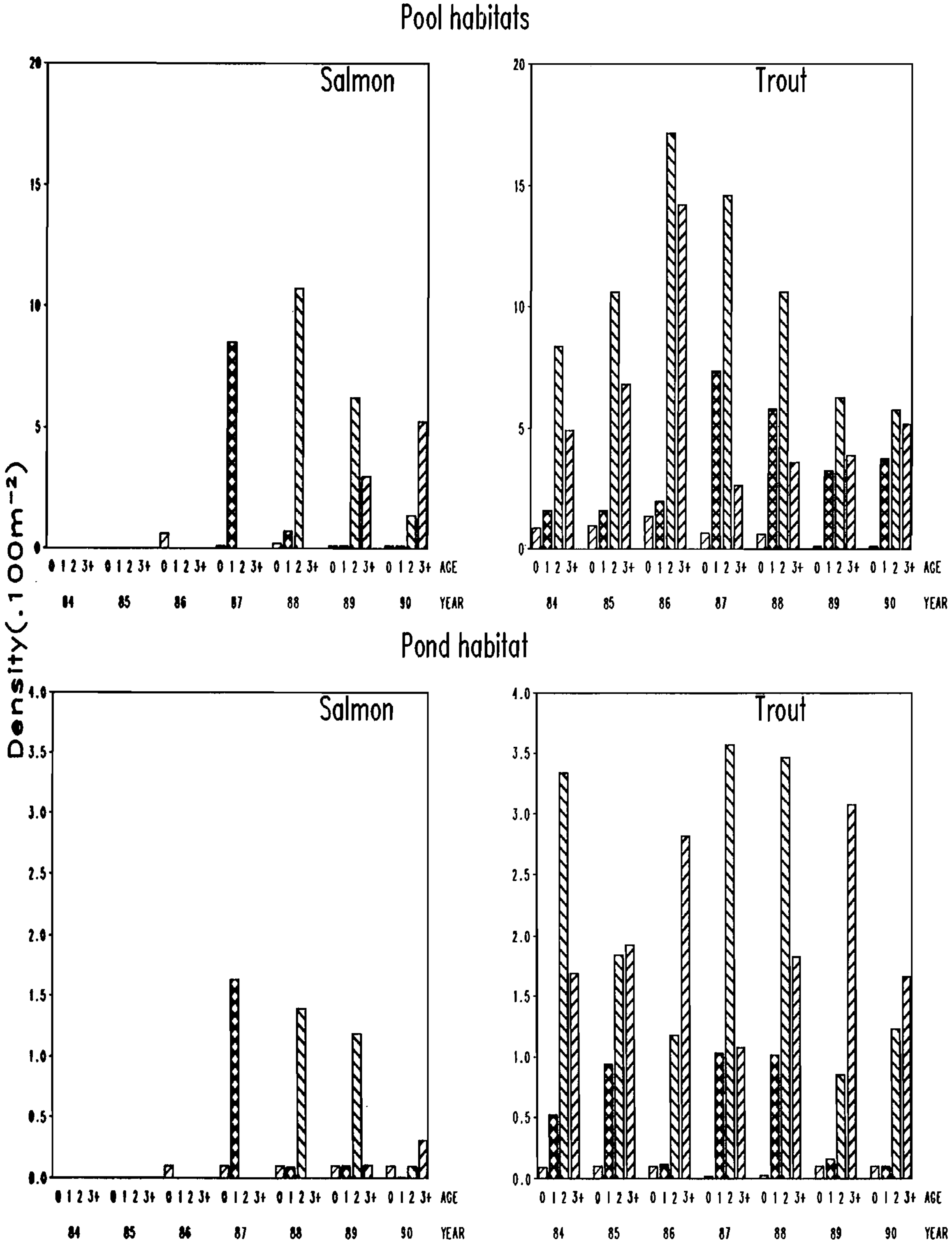

FIG. 10. Changes in densities of salmonids in: (a) pool habitats of Freshwater River; and (b) a pond habitat of Freshwater River.

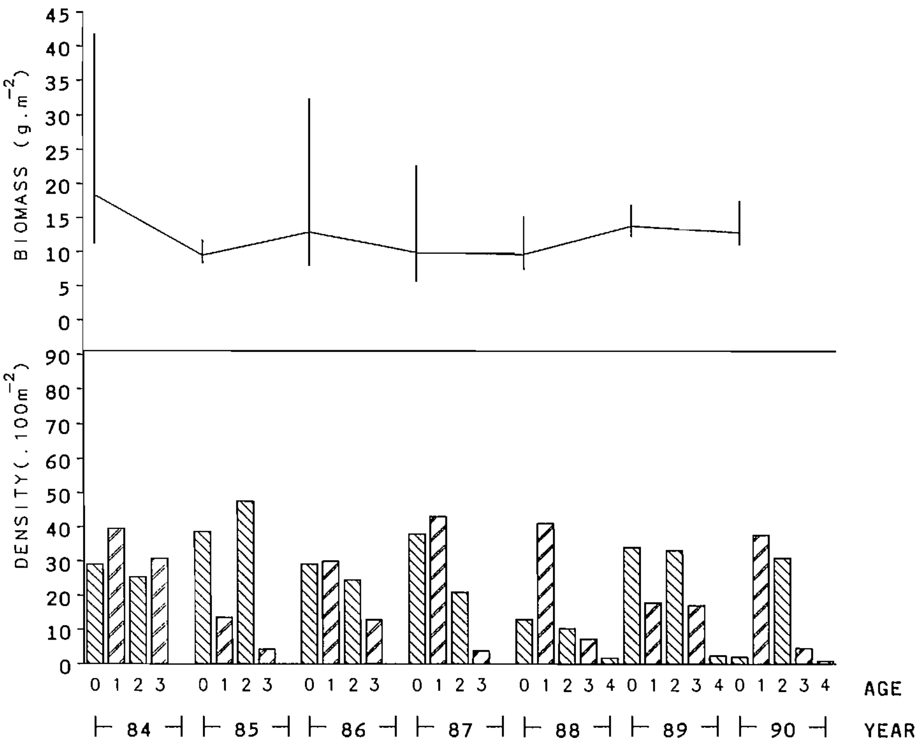

FIG. 11. Changes in densities and biomass of trout in two adjacent riffle habitats of Drook River.

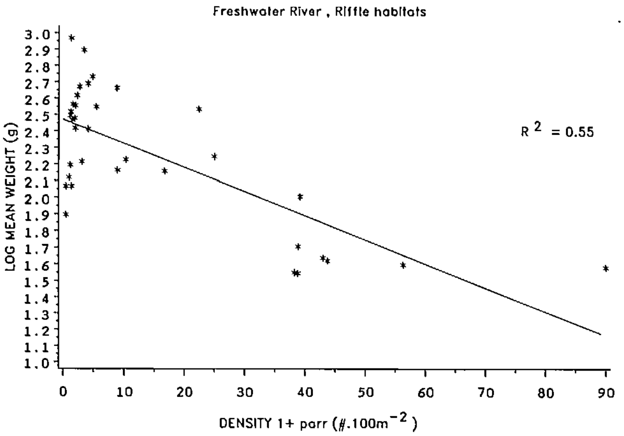

FIG. 12. The mean weight of yearling salmon parr related to densities in riffle habitats of Freshwater River in 1987–90.

Schlosser 1987). There is evidence of similar mechanisms controlling the distributions found in the present study.

Shallow smooth water was shown in experimental stream tanks with natural light to be less preferred by salmon parr and trout than shade cover, deeper water, or a rippled surface (Gibson and Power 1975; Gibson 1978a). A model kingfisher (*Ceryle alcyon*) flying overhead produces escape and fright behaviour in young salmon, showing the importance of avian predators in affecting distribution (Gotceitas and Godin 1993). In an Irish stream underyearling salmon occupied deeper water when brown trout were absent than when present, suggesting competitive or predatory effects from brown trout on distribution at this size (Kennedy and Strange 1986b). Larger food items may be entrained in the main current and settle out in pools (McLay 1970), providing also an advantage for location in pools, likely to be taken by dominant larger fish.

The most conspicuous difference in holding stations between the two species was in height held above the substrate (Fig. 3). Salmon frequently were in contact with the substrate and, in fast flows, characteristically hold stations on the top of a stone, using the hydrostatic pressure of the current on their pectoral and ventral fins to apply themselves to the substrate. In this type of habitat they are aggressive and defend a territory (Kalleberg 1958; Keenleyside 1962). Trout held stations swimming above the bottom, even in the faster currents. It is evident therefore that, in fast water, salmon expend less energy than trout, both by less activity and by occupying slower water near the bottom (Smith 1975). This behaviour allows salmon to occupy a habitat that would be less used by trout (i.e., riffles and runs) and, when food becomes limiting, to displace trout by exploitative competition (Gibson 1973). Trout apparently expand their habitat niche by occupying faster water in the absence of competition with salmon (Fig. 4, Tables 5 and 6).

Pectoral fin lengths of young salmon are longer than those of young brook trout. A similar relationship exists with brown trout in European rivers (Jones 1975) where, similarly to brook trout, brown trout are more associated with pool habitats than salmon. Pectoral fin length does not necessarily indicate relative efficiency in water velocity with the Pacific salmonids steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*), however, where juvenile steelhead trout are regarded as predominantly a riffle dweller, but do not have longer pectoral fins than young coho, which typically occupy the pool habi-

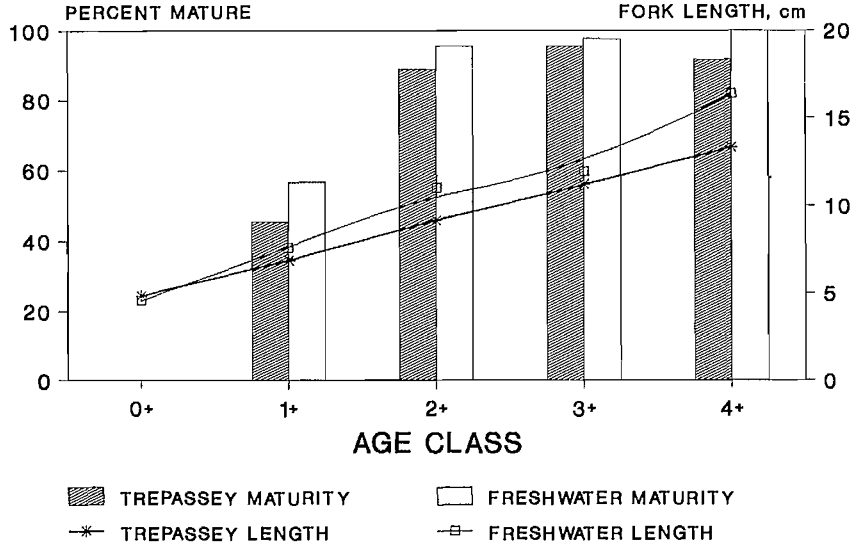

FIG. 13. The relative sizes and proportion of maturing male salmon parr at various ages collected in fluvial habitats of Northeast Trepassey Brook and Freshwater River, 1987–90.

tat (Hartman 1965). However, steelhead trout do not use their pectoral fins specially to apply themselves to the bottom as do young Atlantic salmon (Gibson 1981).

The relative length of the upper jaw of trout is greater than that of salmon. A wider gape would allow trout to take larger food items than salmon (Ringler 1979; Wankowski 1979). Depending on the range in available prey size, some niche separation by feeding therefore would be possible. However, in a river where larger-sized prey were not abundant, poor correlation was found between size of prey taken and gape size, and food eaten by both species was more related to its availability rather than to its size (Thonney and Gibson 1989). Pianka (1981) notes that in an environment with a scant food supply a broad niche maximizes returns per energy unit expenditure, promoting generalization. Stream salmonids are regarded as generalized feeders. Morphological and behavioural differences between salmon and trout therefore are primarily responsible for habitat segregation, rather than niche separation by feeding, although some food differences in relative amounts of items may occur. Immature aquatic insects provide the major food items of both species, although trout in fluvial habitats feed more on surface and on terrestrial items than do salmon parr. Large parr may take more terrestrial insects than small parr and therefore have a diet more like that of the trout, related probably to large parr occupying a habitat more like that of trout (Gibson et al. 1984; Thonney and Gibson 1989).

The response of increased growth rate to lower densities was shown by 1+ parr in riffle habitats (Fig. 12). Young salmon are highly territorial in riffle habitats, but it is unknown whether the increased growth is due to larger territories and more feeding opportunity due to lessened intruder pressure (Dill et al. 1981), less energy expended in territorial defense, or in more food available due to less interception of the drift. All three reasons are possible. Symons (1968) found that parr were less aggressive when food was abundant than when the fish were starved, so that if more food were available, also less energy would be expended in territorial defense. In very productive streams, both densities and growth rates can be high (Gibson and Haedrich 1988) and density-dependent growth may not be apparent when food is not limiting. However, in general, salmon rivers in eastern North America are less fertile than those in Europe and it is probable that food is limiting for much of the year, except in early summer when aquatic invertebrates are abundant prior to and at emergence (Gibson et al. 1984). Elliott (1989) did not observe density dependent growth in a population of brown trout. However, food for most of the year was not limiting. He did find changes in size with changes in density, but this was related to a trimodal growth size frequency, in which selection for a growth pattern was determined at the fry stage. Young salmon have similarly been shown to have a bimodal growth pattern (Thorpe 1977). However, with young salmon, a response to growth with reduction in competitive pressure can occur at the older parr stage (Gibson and Dickson 1984). The advantage of such a response to growth in young salmon is that smolt size can be reached earlier, reducing mortality from the additional year in the river, and output of smolts is stabilized and can be maximixed (Buck and Hay 1984). Density-dependent growth has not been shown to occur after the smolt stage, in the marine environment. Resident trout, however, would continue to be constrained by the river environment, explaining why similar density-dependent growth was not apparent with the brook trout. The latter may, however, respond to low densities or more food by better survival, younger age-at-maturity and increased fecundity (McFadden 1969; Gibson et al. 1976).

Intra-specific competition among salmon also affects rates of maturity of male parr, with resulting changes in survival rates, sex ratios of smolts, and other demographic consequences (Gibson 1978b, 1983; Gibson and Côté 1982; Myers 1984). The faster growth rates of parr resulted in a higher proportion of maturing male parr in Freshwater River than in Northeast Trepassey Brook.

In a previous study, Gibson et al. (1987) found that highest densities and best growth rates of salmon were in riffle habitats, indicating that in the Highlands River this was preferred habitat. If a quantitative relationship could be derived for various size-classes of salmon for density, growth, and productive capacity of a habitat, one of the factors could be calculated if the other two were known, providing a useful model for assessment purposes, related to optimum densities, or quantifying the habitat.

Other studies (e.g., Platts 1974; Blachuta and Witkowski 1990) have shown that salmonids have greater densities and biomass in lower order rivers although individual sizes may be larger downstream, whereas densities and biomass of some other species increase with stream order, related to a continuum of abiotic-biotic factors. Although the paucity of fish species in Newfoundland allows salmonids to occupy a wider range of habitats than occurs where species diversity is higher, the greater biomass and density of salmonids nevertheless is negatively correlated with stream width, and therefore positively with the properties of variables in lower order streams, even in the absence of severe piscine predators and competitors in higher order rivers, demonstrating the importance of abiotic factors.

Evidently, relative species abundance, size distribution, biomass and production are controlled by physical and chemical factors and are modified by inter- and intra-specific competition. Although interspecific competition is likely, with the intensity and direction depending on size of fish, abundance, and type of habitat, it is concluded that salmon, at least in riffle areas, were able to occupy a niche only partly used by brook trout. Where adequate diversity of habitats is present, the two species are ecologically compatible, and are able to exploit the fluvial system, with respect to salmonid production, more efficiently than when only one species is present.

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Effects of Exotic Juvenile Salmonines on Growth and Survival of Juvenile Atlantic Salmon (*Salmo salar*) in a Lake Ontario Tributary[1]

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Restoration of self-sustaining populations of Atlantic salmon (*Salmo salar*) into Lake Ontario may be constrained by biotic interactions between this species and exotic salmonines that have established naturalized populations in streams that historically only supported Atlantic salmon. Wilmot Creek, one of two Ontario streams presently being stocked with juvenile Atlantic salmon, has excellent habitat quality but abundant populations of rainbow trout, coho salmon, and brown trout. To investigate the impact of biological interactions among these species on production of Atlantic salmon smolts, we isolated a series of eight natural side channels to Wilmot Creek for the purposes of manipulating competitor (and predator) abundances. All fish except Atlantic salmon (hatchery-reared parr) were removed from four channels; the other four were left intact as controls. Growth and survival rates of Atlantic salmon parr were significantly greater in the four treated channels. The impact is apparently due to interactions with larger salmon fry (mainly coho) or with yearling rainbow and brown trout, since the smaller, but much more abundant rainbow trout fry were not effectively eliminated from the treated channels. The results suggest that biological interactions may limit rearing success of Atlantic salmon, at least for hatchery produced juveniles. The management implications of these findings will depend in part on the degree to which the results apply as well to naturally produced Atlantic salmon juveniles.

Le rétablissement de populations viables de saumon atlantique (*Salmo salar*) dans le lac Ontario peut être limité par des interactions biotiques entre cette espèce et des salmonidés exotiques qui ont constitué des populations naturalisées dans des cours d'eau qui traditionnellement ne contenaient que le saumon atlantique. Le ruisseau Wilmot, l'un des deux cours d'eau de l'Ontario qu'on repeuple actuellement de saumons atlantiques juvéniles, présente un habitat d'excellente qualité mais des populations abondantes de truite arc-en-ciel, de saumon coho et de truite brune. Pour étudier l'impact des interactions biologiques entre ces espèces sur la production de smolts de saumon atlantique, nous avons isolé une série de huit chenaux latéraux naturels du ruisseau Wilmot pour y manipuler l'abondance des compétiteurs (et des prédateurs). Tous les poissons sauf le saumon de l'Atlantique (tacons d'élevage) ont été enlevés de quatre chenaux; on a laissé les quatre autres intacts pour servir de témoins. Les taux de croissance et de survie des tacons de saumon atlantique étaient nettement supérieurs dans les quatre chenaux traités. Cet impact est apparemment dû aux interactions avec les gros alevins de saumon (principalement le coho) ou avec les jeunes d'un an de truite arc-en-ciel et de truite brune, car les alevins petits mais beaucoup plus abondants de truite arc-en-ciel et de truite brune, car les alevins petits mais beaucoup plus abondants de truite arc-en-ciel n'ont pas été éliminés efficacement des chenaux traités. Les résultats semblent indiquer que les interactions biologiques pourraient limiter le succès de grossissement du saumon atlantique, au moins pour les juvéniles d'élevage. Les incidences de ces résultats sur le plan de la gestion dépendront en partie des possibilités d'application aux juvéniles de saumon atlantique produits dans la nature.

Introduction

The re-establishment of a native species is at best a hopeful undertaking. Typically, the motivation for such efforts derives from a sense that it is a "good thing to do" as a symbol of ecosystem restoration, rather than from compelling scientific arguments that the attempt will be successful. Usually, the ecosystem into which the native species is being re-introduced is very different from the one it formerly occupied, even if the reasons for it past extirpation are no longer extant. This being the case, it is extremely important that the potential ecological constraints to a successful re-introduction be examined, and that this knowledge be used wherever possible to direct the effort towards success.

The attempted re-introduction of Atlantic salmon (*Salmo salar*) into Lake Ontario is a good example. Atlantic salmon were abundant in Lake Ontario during the 18th and early 19th centuries. Deforestation, mill dam construction, and overfishing led to their complete extirpation by the end of the 19th century. Since that time, Lake Ontario and its watershed have undergone immense changes in both physical and biological features. Perhaps most notably in the present context, the fish community composition of the lake and its tributaries is profoundly different. In addition to the native lake trout, several non-indigenous salmonine species have been introduced during the 20th century and are now naturally reproducing. These include chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), rainbow

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trout (*O. mykiss*), and brown trout (*Salmo trutta*). The ability of Atlantic salmon to re-establish self-sustaining populations in Lake Ontario will therefore depend, in part, on the ability of juveniles to cope with the biotic interactions resulting from the co-occurrence of these other salmonines in the tributaries within which they rear.

Biotic interactions, and particularly competition, among salmonids has been the subject of numerous investigations (reviewed by Hearn 1987; Fausch 1988). This literature, while providing numerous examples of competition, has yet to yield sufficiently general models to allow credible prediction of the outcome of interactions between juvenile Atlantic salmon and the other salmonines now present in Lake Ontario's tributaries. To allow assessment of the potential constraint to re-establishment imposed by these interactions, we chose to conduct an experiment at Wilmot Creek, one of the Lake Ontario tributaries into which Atlantic salmon have recently been stocked. This paper presents the results of the first year of this study, in which we examine the interaction of hatchery-reared young-of-year Atlantic salmon with the naturally produced salmonines present in Wilmot Creek. The overall objective of our study is to determine whether these biotic interactions are likely to pose a severe constraint to the re-establishment of Atlantic salmon in Lake Ontario. Given the widespread concerns regarding the impacts on Atlantic salmon of man-caused expansions in the range of other salmonines, the study's findings may have broader implications for the management of Atlantic salmon streams.

Approach and Methods

The overall objective of the experiment was to determine whether the presence of other salmonines, acting as competitors and possibly predators, would reduce the survival and/or growth of stream dwelling juvenile Atlantic salmon to the point where our ability to establish a wild population is seriously affected. We chose to use a field experimental approach to address this objective. The experiment was designed to compare the growth and survival of juvenile Atlantic salmon in the presence and the absence of other salmonines, by removing the latter from experimental sections of Wilmot Creek.

It is well known that the growth and survival of salmonines is influenced by many factors other than competition with and predation by other salmonines. Therefore we felt that an experimental design that only contrasted a single control site (other salmonines present) with a single manipulation site (salmonines removed) would risk confounding due to unavoidable habitat differences between the sites. Instead we chose to establish a total of eight sites, four of which would be manipulated and four left as controls.

The sites were located within small (2–3 m width) side channels off Wilmot Creek, a coldwater stream draining into Lake Ontario approximately 60 km east of Toronto (Fig. 1). Wilmot Creek is a high quality trout stream with substantial groundwater inputs and summer base flows of 0.5 $m^3 s^{-1}$. The catchment is relatively small, with approximately 45 km of stream accessible to migratory salmonines. Gradients average 11 m/km and the substrate is dominated by gravel and rubble, particularly in the upper reaches. Water quality is excellent except in the lowest sections, where temperatures can exceed 25°C. Further upstream temperatures rarely exceed 20°C and conductivity is approximately 500 μmho cm^{-1}.

The side channels were opened up to flow in the summer of 1989 and flushed during the winter and spring of 1990. Considerable differences existed in the physical features of the eight sites; to reduce the likelihood of confounding due to habitat effects we established four pairs of sites based upon a qualitative appreciation of which sites were most similar to each other. One member of each pair was then assigned at random to the control set; the other was designated for manipulation (treatment set).

Fish passage into and out of each site was prevented by the placement of barriers at the top and bottom of the site. The barriers consisted of a 6–8 mm wire mesh screen within a steel frame, placed within the thalweg of the side channel. Plywood wings were attached to the steel frame and secured into the side

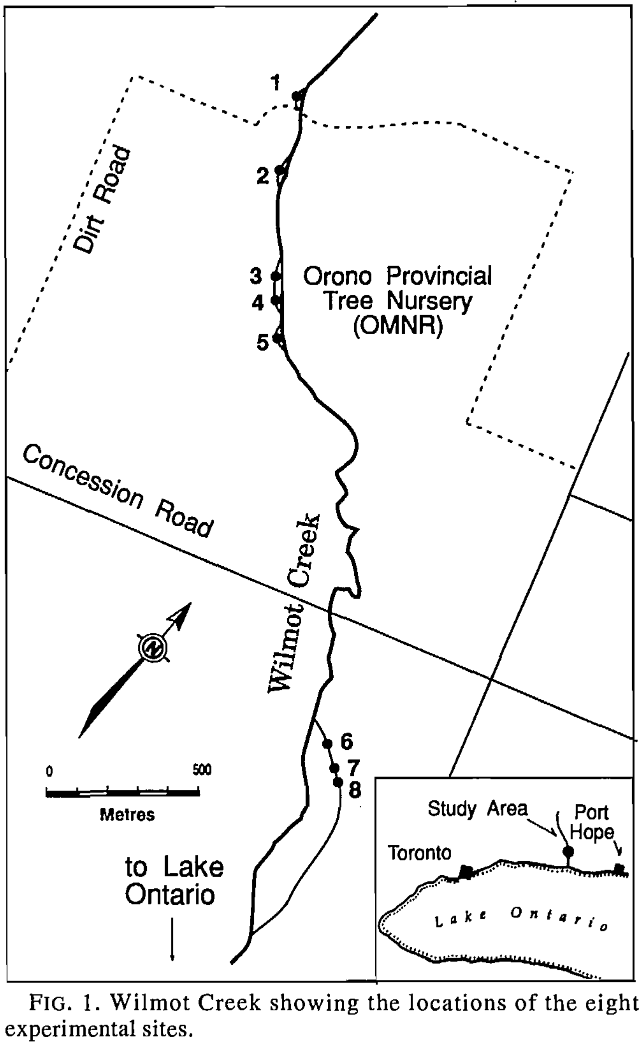

FIG. 1. Wilmot Creek showing the locations of the eight experimental sites.

channel bank on either side of the frame (Fig. 2). Flow under the frame or around the outside of the plywood wings was prevented by burying filter cloth attached to the frame into the substrate and stream bank. The frame at the outlet from each unit also included a triangular trap designed to capture any fish emigrating downstream. Site wetted areas ranged from 80 to 180 m^2.

During June and early July 1990, we mapped the physical habitat of the entire area of each of the eight experimental sites and estimated fish biomass within each unit by the removal method (Zippin 1958) using a Smith-Root Type VII backpack electro-shocking unit. Three passes were used at all sites. We returned all captured fish to the control sites, replacing any mortalities with fish of similar size and species collected from the main channel of Wilmot Creek. Captured fish were not returned to the treatment sites.

Young-of-year (YOY) rainbow trout were not efficiently captured by electrofishing, as evidenced by large numbers still being captured on the final run of the removal procedure. Therefore we continued to electro-fish the treatment sites for several days after the initial manipulations were completed, in an attempt to achieve maximum removal of rainbow trout fry.

On July 6, hatchery-reared underyearling Atlantic salmon were planted into each unit to a density of 1.5 fish/m^2 of wetted area. A sub-sample of 100 fish were weighed and measured to provide an estimate of initial lengths and weights. These fish were not used in the experiments but were assumed to be representative of the planted fish. From this point onward all eight sites were inspected twice daily to clean the screens and check for the presence of fish in the downstream trap. Water temperature and depth were also recorded daily.

Samples of both drifting and benthic invertebrates were collected at the start, midpoint, and conclusion of the experiment from each experimental site and from adjacent main channel sites. Two replicate drift samples were collected at each site over a 24 h period using a 45 cm wide drift net of 0.3 mm mesh size. A T-sampler (Mackie and Bailey 1981) was used to collect four replicate benthos samples from riffle habitats at each site. The samples were sorted immediately and all invertebrates preserved in Kahle's solution for later analysis.

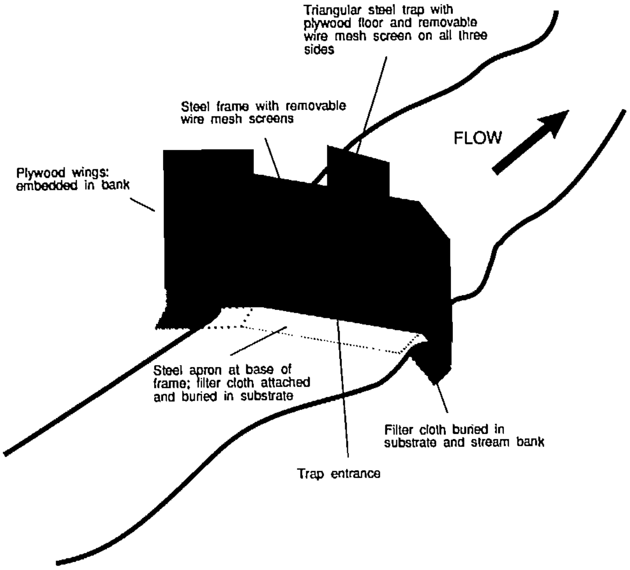

FIG. 2. Schematic of lower gates and screens on experimental sites. A similar structure was used at the upper end of each site, except that it lacked the triangular trap.

The invertebrate samples were analyzed by identifying all organisms to major taxonomic group, measuring lengths on all or a sub-sample (for abundant organisms) using a digitizer, and then converting lengths to biomass using published length-weight relationships and counts by taxonomic group. Finally, we classified all invertebrates into four size categories (following Bowlby and Roff 1986): <0.1 mg; 0.1–1. mg; 1–10 mg; and > 10 mg, and performed all statistical analysis on these size classes, rather than individual taxa.

The experiment was concluded in early October after the fish biomass was re-estimated at each site, again using the removal method. All captured fish were measured and weighed individually (bulk weights for YOY rainbow trout). A sample of 20 Atlantic salmon were kept from each site for more accurate weighing and otolith removal.

Biomass and population estimates were obtained from the electrofishing data using the MICROFISH V3.0 software package (vanDeventer and Platts 1989), which uses a maximum likelihood estimation technique (vanDeventer and Platts 1983). All other statistical analyses were performed using SAS Version 6.03 (SAS Institute Inc. 1988) on an MS-DOS based microcomputer.

Results

The information collected during the habitat mapping of each experimental site was described by 25 parameters (Table 1), representing measures of substrate, cover, and depth/flow attributes. Based on a graphical evaluation of the contrast in these parameters among sites, we selected a subset of 10 for multivariate statistical analysis. Although this variable reduction procedure was not required prior to multivariate analysis, it was done to simplify interpretation of the principal components (see below) that emerged from the analysis. The purpose of the analysis was to determine whether the subjective classification of the experimental sites into treatment/control pairs was supported by a more objective approach.

We used principal components analysis to reduce the 10 habitat parameters down to a smaller number of principal components that explained most of the variation among experimental sites. A scatter plot of the first two principal components for the eight sites (Fig. 3) shows a clear separation of at least three of the four pairs of sites. Pair C (sites 5,6) had similar first principal component values, but differed on the second axis. The second component was a depth/morphometry axis; site 5 had a relatively great mean depth and a small amount of marginal flat areas, by

TABLE 1. Habitat attributes measured at each of the eight experimental sites. Attributes with an asterisk were used in the principal components analysis. Note that pool types 1 and 2 were lumped for the analysis, as was pool type 4 with runs, and gravel with rubble.

	Experimental Site							
Habitat Attribute	1	2	3	4	5	6	7	8
Total Length (m)	49	33	45	47	47	67	54	65
Mean Width (m)	3.78	2.38	2.44	2.56	2.89	1.87	2.41	1.58
Mean Depth (cm)*	14.97	19.30	40.25	36.53	40.82	21.42	32.32	29.00
Depth/Flow	*% of Total Area by Habitat Category*							
Flats	12.55	13.04	7.52	8.32	5.75	15.84	28.87	28.52
Pool 1 (poor)*	0.00	0.00	7.34	0.00	5.16	0.00	0.00	0.00
Pool 2 (medium)	7.99	0.95	7.7	19.80	4.57	18.95	0.00	1.71
Pool 3 (good)*	39.96	16.79	36.07	29.45	13.59	8.58	14.93	10.00
Pool 4 (excel.)*	0.00	8.91	9.24	9.23	6.34	24.10	35.99	0.24
Runs*	3.24	11.13	27.46	22.63	46.78	6.19	12.89	45.34
Marginal flats*	8.42	16.73	4.58	5.07	1.62	7.38	5.97	13.46
Riffles*	27.85	32.44	0.00	5.49	16.21	18.95	1.35	0.73
Substrate	*% of Total Area by Habitat Category*							
Silt*	17.17	16.83	21.88	14.77	1.59	25.52	31.75	14.44
Sand*	19.44	32.06	43.07	47.38	32.20	28.17	32.90	68.78
Gravel*	38.36	45.40	26.86	32.69	60.62	36.99	17.05	5.31
Rubble*	23.62	2.95	2.36	0.28	0.92	0.83	0.04	0.00
Boulder	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Clay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Detritus	2.07	3.68	2.67	4.27	1.27	2.62	5.64	11.47
Cover Types	*% of Total Area by Habitat Category*							
Undercut*	1.46	3.18	2.81	2.91	6.56	5.67	0.19	0.23
Logs	2.37	9.13	4.53	3.33	5.01	5.95	1.15	5.35
Log Jams	0.16	0.95	0.00	0.00	0.74	0.60	0.00	0.00
Boulder	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Roots	0.40	0.64	0.50	2.00	0.00	0.00	0.19	0.00
Brush	5.29	0.00	0.00	1.66	0.00	0.00	0.00	0.00
Total Cover*	9.69	13.91	7.84	9.90	12.30	12.21	1.54	5.59

comparison to site 6 (see Table 1). We also derived a discriminant function based on the first two principal components; the function successfully classified all eight sites into the four pairs assigned by us subjectively prior to the experiment. Therefore the objective approach supported our subjective classification of the sites into four pairs with similar habitat characteristics.

Prior to the experiment, fish biomass in all eight experimental sites was dominated by salmonines (Fig. 4: Upper). The only non-salmonine fish present in significant numbers or biomass was the mottled sculpin (*Cottus bairdi*). This is typical of all but the lowest sections of Wilmot Creek (M. Jones, unpubl. data). The pre-experiment electrofishing was successful in eliminating all potential competitors or predators from three of the four treatment sites (Fig. 4: Middle) except sculpins and YOY rainbow trout (Fig. 4: Lower). At site 7 the biomass of other salmonines was greatly reduced, but a few yearling brown and rainbow trout remained. The presence of YOY rainbow trout at the treatment sites at the conclusion of the experiment, despite our extra efforts to remove them at the start, would suggest that the wire mesh screens were not effective at excluding very small rainbow trout, at least during the early stages of the experiment when they were, on average, less than 45mm in total length. We suspect that sculpins were simply not effectively captured within the side channels during the removal efforts.

The Atlantic salmon fry were very large (mean total length: 72.2 mm; C.V.: 15.54%) and in good condition at the start of the experiment, having been raised for 4 months in quarantine at the Ontario Ministry of Natural Resources hatchery at Normandale. Growth during the experiment was very poor, however, at all eight experimental sites. For example, in the control sites the length increment of Atlantic salmon was, on average, less than half that of other salmonines (11.6 mm vs. 23.6 mm; Fig. 5). Growth in the treatment sites was better (16.0 mm), but still less than that observed for other salmonines in the control sites.

Despite the overall poor performance of the Atlantic salmon fry, there were significant differences in growth rates among the experimental sites (Table 2). As anticipated, physical differences among sites were of considerable importance ($P < 0.001$). Even after accounting for habitat effects, however, the treatment effect was significant ($P < 0.02$). Thus the results suggest that the presence of other salmonines led to

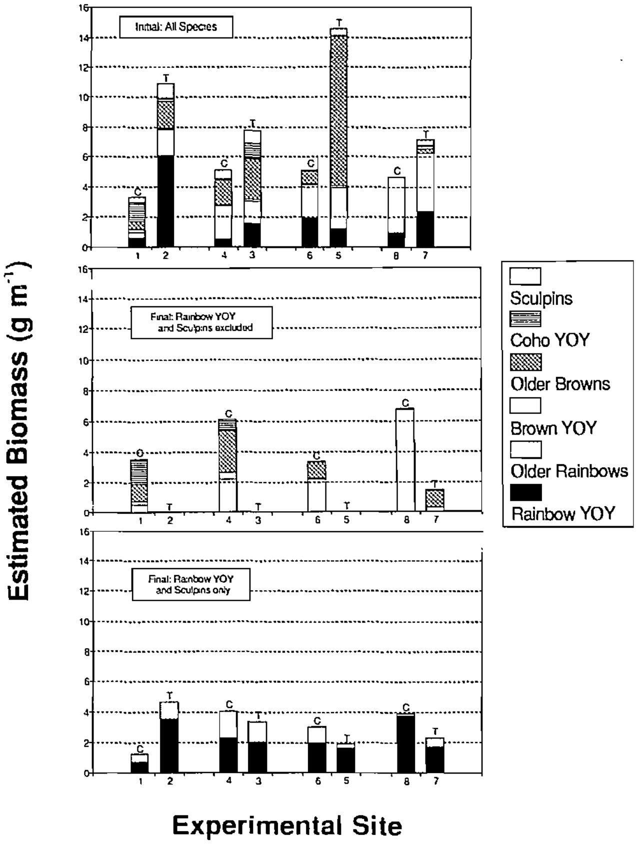

FIG. 4. Fish biomass estimates for each of the experimental sites based on electrofishing surveys. *Top*: biomass for all species at the start of the experiment. *Middle*: biomass for all except YOY rainbows and sculpins at the end of the experiment. *Bottom*: YOY rainbow and sculpin biomass at the end of the experiment. The T and C symbols differentiate treatment and control sites.

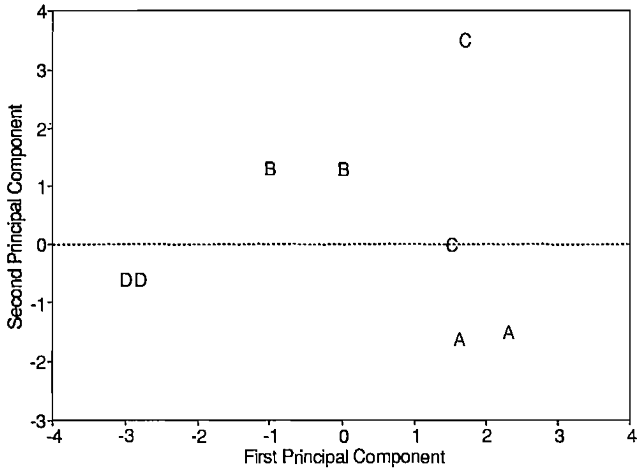

FIG. 3. Scatter plot of the first and second principal components of 10 habitat variables measured at each of the eight experimental sites. Each pair of sites is designated by a different character symbol.

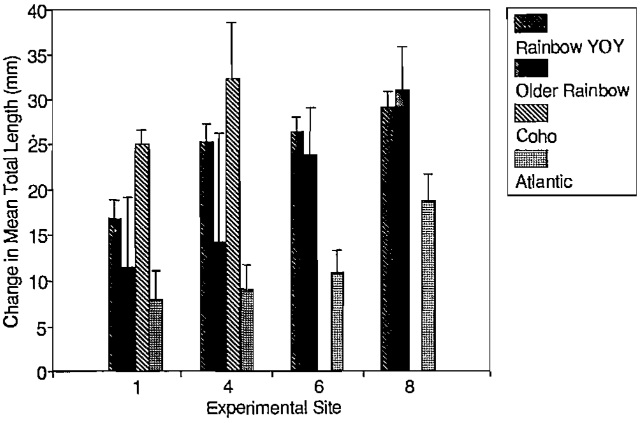

FIG. 5. Changes in mean total lengths of salmonids over the duration of the experiment within each of the control experimental sites. Also shown (above each bar) is the standard error of each change in mean length.

reductions in Atlantic salmon fry growth during July-September. Since YOY rainbow trout were present in all sites, this implies that interactions with larger salmonines (YOY coho, yearling rainbows, and older browns) had this effect.

Survival of Atlantic salmon, as computed by comparing initial numbers stocked to the estimated abundance at the conclusion of the experiment, was also higher at the treatment sites in three of four comparisons (Table 3). Overall, there were significantly fewer survivors relative to initial numbers in the control sites than the treatment sites (controls: 23.6% survival; treatments: 45.9% survival; chi-square $P < 0.001$). The habitat effect was also significant (chi-square $P < 0.001$), but in contrast to the growth data, here the treatment effect was of greater magnitude than the habitat effect.

Although both growth and survival were lower at the control sites, they are not closely correlated (Fig. 6). For example, growth was greatest at sites 7 and 8 (pair D), whereas survival was lowest at site 8. This suggests that the causes of the reductions in growth and survival are not the same, and that different factors acted more or less strongly at different

TABLE 2. Comparison of growth rates (changes in mean total lengths from the start to the end of the experiment) of Atlantic salmon parr, including the results of 2-way ANOVA with factors "habitat group" (4 levels) and "treatments" (2 levels).

Site	Type	Habitat Group	Change in Mean Total Length
1	C	A	7.95
2	T	A	10.54
3	T	B	16.16
4	C	B	8.99
5	T	C	11.72
6	C	C	10.76
7	T	D	25.39
8	C	D	18.69

Source	DF	Sum of Squares	Mean Square	*F* Value	Pr > *F*
Model	7	5555.	794.	5.77	0.0001
Habitat	3	4447.	1482.	10.78	0.0001
Treatment	1	803.	803.	5.84	0.0167
Interaction	3	305.	102.	0.74	0.5299
Error	166	22818.	137.		
Total	173	28373.			

TABLE 3. Comparison of survival rates of Atlantic salmon parr during the experiment, including the results of a contingency table analysis with factors "habitat group" (4 levels) and "treatment" (2 levels).

Site	Type	Habitat Group	Number at Start	Number at End	Survival
1	C	A	278	55	0.198
2	T	A	118	49	0.415
3	T	B	166	57	0.343
4	C	B	205	84	0.410
5	T	C	206	125	0.607
6	C	C	200	38	0.190
7	T	D	198	86	0.434
8	C	D	130	17	0.131

Contingency Table Analysis

Factor	df	X^2	Pr > X^2
Habitat Group	3	21.48	<.001
Treatment	1	82.87	<.001

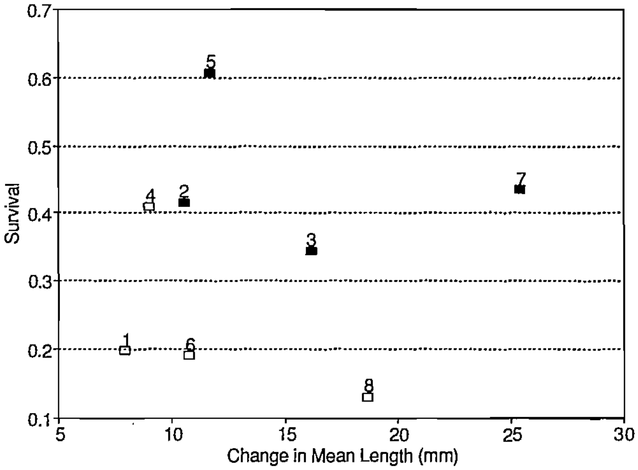

FIG. 6. Atlantic salmon survival versus growth for each of the eight experimental sites. Each point is labelled by site number. Open squares are control sites; closed squares are treatment sites.

sites. Nevertheless, survival and growth were both, on average, lower in the sites where the biomass of other salmonines was not reduced due to manipulation.

Using ANOVAs on log-transformed data we found that abundance of benthos showed little differences ($P > 0.5$) between the control and treatment sites whereas drift was significantly less abundant ($P < 0.05$) in the control channels in late August at the midpoint of the experiment (Table 4). In contrast, the habitat effects were greater for the benthos and maximal at the end of the experiment (Table 4, $P < 0.01$), while habitat effects on drift abundance were modest and tended to diminish over time. Finally, the drift and benthos samples taken from adjacent main channel sites did not indicate large, consistent differences between main channels and the side channels. We obtained similar results when biomass, rather than abundance, of organisms was used as our measurement variable.

Discussion

The experimental reduction of other salmonine competitors and predators in Wilmot Creek resulted in significant increases in both the growth and survival of underyearling Atlantic salmon over a three month period from July through September. This study therefore supports the hypothesis that, during their first growing season, the presence of an abundance of other salmonines has a negative impact on Atlantic salmon juveniles of hatchery origin.

Although our results indicate that other salmonines influence the growth and survival of juvenile Atlantic salmon, this study does not provide a true indication of the significance of interspecific competition among salmonines. As Fausch (1988) pointed out, the signficance of interspecific competition can only be evaluated by comparing it to intraspecific competition. In this study, the treatment sites, by virtue of the removal of other salmonines, had lower *overall* biomass than the control sites. We do not know whether Atlantic salmon growth and survival would have been similarly reduced in the treatment sites if the other salmonine biomass had been *replaced* by a similar biomass of juvenile Atlantic salmon, rather than simply *removed*. Nevertheless, our design was suitable given the objectives of this study, namely to determine whether the non-native salmonids present in Wilmot Creek affect the growth and survival of juvenile Atlantic salmon.

Other studies of Atlantic salmon interactions with other salmonines have produced contrasting conclusions. For example, Gibson and Cunjak (1986) concluded that Atlantic salmon populations were not at risk from brown trout introductions provided riffle habitat is abundant. Hearn and Kynard (1986) concluded similarly that competitive interactions between Atlantic salmon and rainbow trout, while giving rise to niche separation, were unlikely to have severe population consequences. In contrast, and in the only study to date that has *directly* investigated and reported on population-level consequences of species interactions involving Atlantic salmon, Kennedy and Strange (1986) found that Atlantic salmon growth and survival was significantly higher in a stream section from which brown trout had been removed than in a control section.

TABLE 4. Invertebrate density and biomass data from the eight experimental sites sampled in late August and September. Type refers to control (C) or treatment (T). Habitat groups are as in Fig. 3.

			Late August		Late September	
Site	Type	Habitat Group	Denisty (#/m^3)	Biomass (mg/m^3)	Density (#/m^3)	Biomass (mg/m^3)
			Drift			
1	C	A	0.182	0.174	0.121	0.562
2	T	A	0.323	0.480	0.423	0.628
3	T	B	0.200	0.150	0.027	0.090
4	C	B	0.075	0.078	0.141	0.120
5	T	C	0.575	0.293	0.110	0.213
6	C	C	0.037	0.028	0.233	0.136
7	T	D	0.110	0.455	0.179	0.309
8	C	D	0.028	0.143	0.063	0.293
			Benthos			
1	C	A	6755	4.328	409	0.130
2	T	A	14086	4.512	625	3.648
3	T	B	3654	3.778	1611	0.732
4	C	B	12499	3.289	7019	6.109
5	T	C	8197	3.338	8389	7.433
6	C	C	3437	0.579	3149	3.672
7	T	D	1611	2.002	1082	1.349
8	C	D	1442	2.256	1082	4.500

It is likely that habitat differences, as suggested by Gibson and Cunjak (1986), are the key to reconciling these different results. In a section of stream where habitat favours one species over another, the less-favoured species (e.g., YOY Atlantic salmon in a section with relatively little riffle habitat) will be particularly vulnerable to competitive interactions, since individuals are forced to occupy less-than-ideal habitats. Similarly, habitat (especially cover) will play a key role in determining the vulnerability of a species to predation. In the present study we found that habitat differences were at least as important as biotic differences in influencing growth and survival rates of Atlantic salmon (Tables 2,3). In fact, had we not stratified our experimental sites into treatment/control pairs with similar habitat characteristics, we would probably have failed to detect significant treatment effects, at least on growth rates. This study therefore underlines the importance of considering *both* the physical *and* biological environment of a species when investigating processes influencing population dynamics. Findings from experiments in which only two sites (one treatment, one control) are compared must be interpreted with considerable caution.

Although the study design was intended to result in the effective removal of all salmonines other than Atlantic salmon from the treated sites, we were unsuccessful in removing the most abundant group — YOY rainbow trout. By the end of the experiment (and presumably throughout it) YOY rainbow abundance was comparable in all eight sites. Therefore the biological interactions suggested by our findings cannot be attributed to competition between YOY Atlantic salmon and YOY rainbow trout.

This study does not provide conclusive evidence of the mechanism by which growth and survival were affected by the treatment. Both (fish) predation and competition may have been involved. The relatively large size of the Atlantic salmon at the start of the experiment put them in a size category more comparable to YOY coho salmon and brown trout, and even the smaller yearling rainbow trout, all of which were successfully removed from the treatment channels. The observation of relative reductions in drift biomass and abundance in the control sites during the experiment is consistent with the hypothesis that competition for food among these groups has played a role. On the other hand, increased survival also resulted from the treatments, which implies that predation by older brown and rainbow trout may be a factor.

It seems likely that more than one mechanism is involved, because the growth and survival effects did not show the same pattern among habitat types (Fig. 6). Survival was poorest in habitat pairs A and D (sites 1,2 and 7,8), whereas growth was greatest in pair D. Habitat pairs A and D were characterized by being shallow relative to pairs B and C. Further, pair D had relatively little cover compared to the other three pairs. The lack of depth and cover may have resulted in increased vulnerability of Atlantic salmon to predation in these sites. Pair D was also distinguished from the other pairs by a relatively open, deciduous canopy instead of a more closed, conifer dominated canopy. This may have contributed to the elevated growth rates at these sites, via increased allochthonous food inputs (e.g., terrestrial insects), although this is not evident from the drift samples.

We suspect that the findings of this study are strongly influenced by the use of hatchery-reared Atlantic salmon, rather than wild fish. Sosiak et al. (1979) found feeding rates of hatchery Atlantic salmon parr to be less than for wild fish collected from the same stream 1–3 months after release of the hatchery fish. Thus the poor growth of Atlantic salmon observed in all experimental sites is probably due to their inexperience in foraging for stream invertebrates, particularly in the presence of other salmonines. Even in the treated sites, YOY rainbow trout were abundant and may have suppressed Atlantic salmon growth.

The poor performance of hatchery fish may have important implications regarding Atlantic salmon stocking. For streams already containing juvenile salmonines, we would predict poor growth and survival of fish stocked as fingerlings after having become conditioned to a hatchery feeding environment, if they are too small to emigrate successfully from the stream. It would be preferable to either stock them in the spring either as swim-up fry or at a large enough size (> 15 cm) that they are likely to emigrate soon after stocking. Although much higher mortality is to be expected when fry are stocked, the increased numbers that can be economically produced for fry planting may compensate, leading to higher yields per dollar invested in culture. In addition, the latter strategy (smolt stocking) may lead to increased adult straying and therefore poorer spawning success in the target rivers, due to a lack of imprinting.

Averaged across all four pairs of sites, growth was 27% and survival 48% lower in the control than treatment sites. If these figures represent a reasonable approximation of the reductions in YOY Atlantic salmon growth and survival to be expected on an annual basis in the presence of other salmonines, they imply a substantial population-level impact. Without further experiments, however, it would be unreasonable to conclude that Atlantic salmon re-establishment in Wilmot Creek (or other Lake Ontario salmonine streams) will be severely constrained by biotic interactions with other naturalized salmonines. Further studies, using wild salmon and ideally extending over longer time periods, should allow us to decide whether interventions (i.e., establishment of “Atlantic-salmon-only” streams or stream reaches) are needed to ensure the return of the once abundant and valued species to the Lake Ontario watershed.

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Habitat Measurement and Population Estimation of Juvenile Atlantic Salmon (*Salmo salar*)

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Juvenile Atlantic salmon (*Salmo salar*) production area for the Stewiacke, Musquodoboit and St. Mary's rivers, Nova Scotia, was measured using aerial photography and orthophotographic maps. Water surface area was defined by reaches between 5 m contour intervals. Accuracy and bias of the remote sensed data were determined by stream surveying and correction formulae were calculated for area and stream gradient. A sampling procedure, weighted by stream gradient and distance above the head of tide, selected reaches for electrofishing parr populations. Densities of total age-1+ and age-2+ parr were higher at moderate, 1.0 to 1.5% map gradient or 1.2 to 1.4% stream gradient, and lower in the 0.0 to 0.12% map gradient category. Areas greater than 2.5% map gradient were seldom encountered and low densities were found in reaches greater than 2.0% map gradient. The in-stream survey technique increased the ability to detect differences in parr populations between temporally and/or spatially separated reaches.

Total river population estimates of parr were determined annually by four methods and populations in one tributary were compared to smolt counts. Exponential and quadratic models more accurately predicted total parr populations than models based on means or probability density functions or models with constants which overestimated parr in the lowest gradient reaches. Correlation between parr populations and an index of escapement was highest for positively biased estimates based on mean parr densities . Observation and analysis of variance by tributary support the hypothesis of separate and stable populations by tributary. Estimates of adult salmon production based on juvenile populations indicated equivalent production for the Stewiacke and St. Mary's rivers despite the two-fold difference in area. Negative exponential models are recommended to address questions of habitat preference and absolute population estimation, while quadratic models are recommended for statistical comparisons. Estimates based on remote sensed data have lower precision because of error in photogrammetric interpretation of widths and gradients. A major advantage of the gradient modeling technique is objective estimation of actual and habitat-sensitive potential production over large geographic areas.

L'aire de production des juvéniles du saumon de l'Atlantique (*Salmo salar*) des rivières Stewiacke, Musquodoboit et St. Mary's (Nouvelle-Écosse) a été déterminée par examen de photographies aériennes et de cartes orthophotographiques. La superficie des plans d'eau a été établie par tronçons entre les intervalles de courbes de niveau de 5 m. L'exactitude et le biais des données de télédétection ont été déterminés par des relevés sur place et des formules de correction ont été élaborées pour les superficies et les gradients des cours d'eau. Une procédure d'échantillonnage pondérée par le gradient des cours d'eau et la distance en amont de limite de la marée a permis de choisir les tronçons pour la pêche électrique des tacons. Les densités des tacons des âges 1+ et 2+ étaient plus élevées dans les zones de gradients des cartes moyens de 1,0 à 1,5 % ou dans les zones de gradients des cours d'eau de 1,2 à 1,4 % et plus faibles dans les zones de gradients des cartes de 0,0 à 0,12 %. Les zones à gradients des cartes supérieurs à 2,5 % étaient rares et les densités étaient faibles dans les tronçons de gradients des cartes supérieurs à 2,0 %. La technique des relevés en cours d'eau a permis d'accroître la possibilité de déceler des écarts entre les populations de tacons de tronçons distincts, tant dans le temps que dans l'espace.

Des estimations annuelles de la population totale de tacons des cours d'eau ont été obtenues par quatre méthodes et les populations d'un tributaire ont été comparées aux valeurs de dénombrement des saumoneaux. Les modèles de type exponentiel ou quadratique permettaient d'obtenir une prévision plus exacte des populations totales de tacons que les modèles basés sur des fonctions de densités moyennes ou probabilistes ou les modèles comportant des constantes qui surestimaient le nombre de tacons dans les tronçons de gradients plus faibles. La corrélation entre les populations de tacons et un indice de l'échappée s'est avérée la plus élevée pour les estimations à biais positifs reposant sur des densités de tacons moyennes. L'observation et l'analyse de la variance par tributaire appuient l'hypothèse selon laquelle il existe des populations distinctes et stables dans les tributaires. Les estimations de la production de saumons adultes faites à partir des populations de juvéniles indiquaient des productions équivalentes dans les rivières Stewiacke et St. Mary's, cela en dépit d'une différence de superficie du double. L'auteur recommande les modèles exponentiels négatifs pour l'étude des préférences d'habitats et l'estimation des populations absolues, mais les modèles quadratiques pour les comparaisons statistiques. Les estimations obtenues à partir des données de télédétection sont moins exactes à cause d'erreurs liées à l'interprétation photogrammétrique des largeurs et des gradients. L'un des importants avantages de la technique de modélisation par gradients réside dans l'estimation objective de la production réelle en fonction de l'habitat dans de grandes zones géographiques.

Introduction

Production of juvenile Atlantic salmon (*Salmo salar*) is dependent on the number of eggs deposited (Paloheimo and Elson 1974; Watt and Penny 1980; Chadwick 1982), the quantity of habitat (Elson 1957), and growth rate. Growth rate has been shown to vary with a range of environmental factors such as chemical water quality (LeCren 1972), temperature (Allen 1941), and photoperiod (Higgins and Talbot 1985) or the interaction of these variables, e.g., photoperiod and temperature (Metcalfe and Thorpe 1990). Carrying capacity for any stream to produce smolts is a function of these variables. Rearing area (habitat) accounted for 62% of the variation in mean sport catch in rivers of Newfoundland and Labrador and 86% of the variation in catches for Maritime rivers (Chadwick 1985). Therefore, accurate assessments of Atlantic salmon stocks are dependent on accurate habitat surveys of complete river systems.

Atlantic salmon are distributed over a wide geographical range in eastern North America from Ungava Bay in the north to the Connecticut River in the south. Proportionate distribution of habitat varies considerably within a river system and among river systems. Improved estimates of salmon production must therefore rely on surveys which discriminate habitat. Because the range of Atlantic salmon is extensive, complete quantitative surveys of habitat are only practical through remote sensing.

Salmonid population distributions have been described as contagious (Bohlin et al. 1981) and stratified sampling with respect to biotope was suggested as one way to reduce the rather large (0.70) coefficient of variation between locations. Multi-stage sampling designs have also been suggested as one way of reducing variance when attempting to estimate the standing population of fish in small streams (Hankin 1984). Intensive sampling programs incorporating both these strategies (Shackley and Donaghy 1992) can adequately estimate the standing population of parr but are expensive and, like river-specific stock and recruitment relationships, the information obtained is not directly transferrable to other river systems.

Distribution of juvenile Atlantic salmon within streams has been associated with a variety of physical attributes of streams, such as water depth (Egglishaw and Shackley 1982), water velocity (Symons and Heland 1978), and substrate size (Rimmer et al. 1984; Morantz et al. 1987). However, most of these variables are unobtainable for entire or large portions of streams and therefore are not suited to widespread habitat descriptions. Hydrological models such as the Chezy or Manning formulae relate velocity to depth, bottom roughness and gradient (Dunne and Leopold 1978) demonstrating that most of these attributes are interdependent and functionally related.

The possibility that a remotely measured parameter such as stream gradient could account for considerable variance in juvenile densities and distribution was postulated by Symons and Heland (1978). Attempts to relate age-1+ and older parr densities to gradient were unsuccessful (Symons and Helland 1978; Kennedy and Strange 1982). However, area-weighted gradient of continuous ecological units explaining 79% of the variation at eight locations on the Stewiacke River, N.S., (Amiro 1984) provided the incentive to examine the hypothesis further. Stream gradient, a physical attribute potentially differentiating habitat preference for juvenile salmonids, is measurable both proximately (in-stream surveys) and by remote sensing. If stream gradient is a suitable indicator of juvenile salmon habitat, then a continuous description of stream gradient for an entire river system could allow the derivation of better estimates of standing populations of juvenile salmon. Adjusting this population to an optimum number would allow custom-fitted estimates of required egg deposition for each river system.

This paper examines the accuracy of remote-measured stream surface area and gradient and tests the hypothesis that juvenile Atlantic salmon, collected in the Stewiacke, St. Mary's, and Musquodoboit rivers (Fig. 1), were systematically distributed with respect to stream gradient. Usefulness of the survey techniques and parr distribution functions is explored through development of parr population models based on stream gradient and area, and calibrated by electrofishing. Accuracy and precision of total population estimates of combined age-1+ and age-2+ parr (total parr) are examined and examples of some applications of the technique, such as assessment of inter-annual population variation and inter-river production ranking, are shown.

Materials and Methods

Remote Surveys of Streams

Numerical longitudinal profile descriptions of each stream of the Stewiacke, Musquodoboit and St. Mary's rivers, N.S., (Fig. 1) were derived from digital measurement of stream lengths between 5 m contour intervals on 1:10,000 orthophotographic maps (L.R.I.S., 1978, from 1973 photography).[1] Water surface areas between contour lines crossing the streams (reaches) were calculated from the product of digitally measured stream lengths and mean widths measured from 1:10,000 colour aerial photographs.

Sampling intervals for width measurements were generated on data forms according to an algorithm which required a minimum of two widths within reaches less than 50 m (using the first measurement of the next reach for calculating an average), or width measurements approximately every 50 m for reaches up to 1.6 km (maximum of 32 measurements). The interval for sampling reaches longer than 1.6 km was increased by 10 m until 32 or fewer samples were required. Distance

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[1] Land Registration and Information Systems, Surveys and Mapping Division, Summerside, P.E.I.

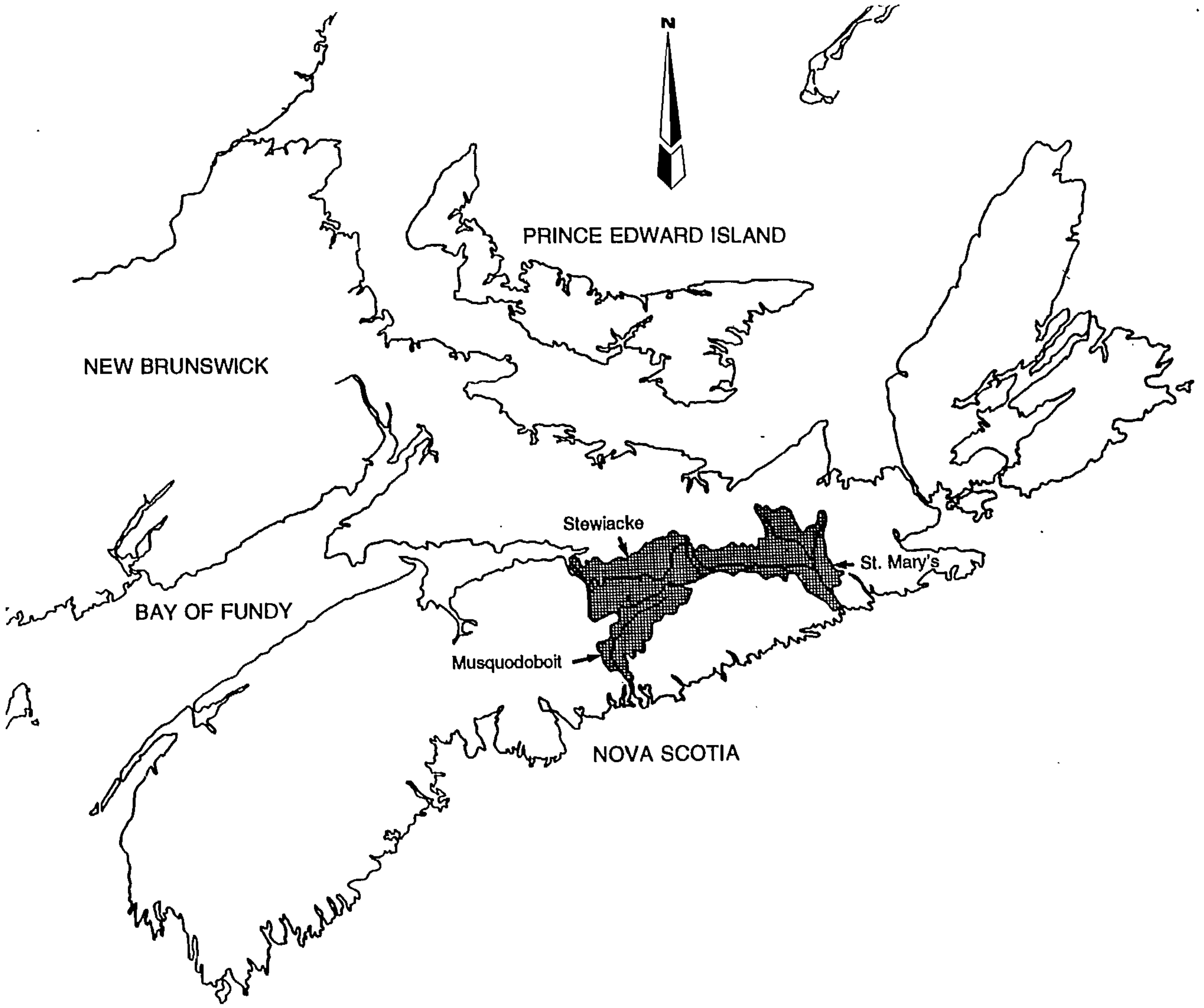

FIG. 1. The locations of the Stewiacke, Musquodoboit and St. Mary's rivers in Nova Scotia.

between width samples was the integer value of the length of the reach divided by the estimated number of sampling intervals. Widths were measured using a 6× monocular comparator equipped with a 10^{-1} mm divisional line reticle.

Reaches were located on the air photos, using stereo scopes when necessary, by comparing topographic attributes with those on orthophotographic maps. Widths of reaches were recorded continuously upstream until the map grade exceeded 15%, unless bridged by a fishway. Where viewing of a stream was obstructed by overhanging cover or shadow, width measurements were attempted for the next four reaches and if no further measurements were possible the survey was terminated for that stream. Average widths were interpolated where widths could not be measured for three or less reaches. When the first four reaches of a stream were not viewable on the photos and the stream consisted of many reaches and confluences, a search for an unobstructed view was made upstream on the aerial photos. If a stream width was resolvable, then the survey was continued and widths for the non-viewable portion of the stream were extrapolated from downstream reaches. Reaches were assigned a control code specifying its potential contribution to production of salmon parr, its ecological class, e.g., stream, lake, or estuary and which widths were complete or interpolated.

Width measurements taken from photographs were converted to meters using the exact scale factor calculated for each photo according to the flying height, focal length and ground elevation (value of the lower contour of the reach). Because photos were taken on various dates and flow conditions, mean widths of reaches were adjusted to the standard summer low discharge reflecting the minimum area available for parr production.

Daily water gauging data over as many years as available were used to calculate the Average Daily Flow (ADF in cubic metres second^{-1}) and the Mean Summer Low (MSL) for the months July, August and September. A width correction for river discharge condition on the day of photography was based on a regression between log % change in mean top width (based on 100% ADF) on log % ADF for two tributaries of the North Platte River, Wyoming (data in

Wesche 1973). That equation (log $Y = 8.6897$*log $X - 15.4158$, $r^2=0.9035$; $p = 0.001$), which excluded values < 12.5% of ADF because these values are below most MSL flows found on unregulated streams, was used to calculate the percent change in top width for the estimated MSL as well as the percentage change in top width for the date of the photo. The ratio between the % of ADF top width for MSL and % of MSL top width for the photo day was the width correction factor.

On-site Stream Surveys

Locations for stream surveys were randomly selected from reaches classified according to 11 map gradient categories: (1) 0.0–0.12%, (2) 0.121–0.25%, (3) 0.251–0.50%, (4) 0.501–1.00%, (5) 1.001–1.50%, (6) 1.501–2.00%, (7) 2.001–2.50%, (8) 2.501–3.0%, (9) 3.001–3.5%, (10) 3.501–5.0% and (11) >5.001%. Groups of reaches were stratified by map grade category and by 10 km distance intervals from approximate head of tide. Selection of reaches for proximate surveying was weighted by the proportion of the total water surface area represented by a distance and gradient cell.

Stream surveys of selected reaches for comparison to areas derived by map surveys were conducted at reaches located in the field using orthophoto maps and colour aerial photographs. Surveying proceeded with regard to "ecological units", i.e., sections of streams with similar bottom and water surface characteristics (Amiro 1984). Stream width (wetted width) was measured at the beginning, end and every 30 m or midpoint of an ecological unit. Widths and lengths were measured to the nearest centimeter with a fibre measuring tape. Depths were measured to the nearest millimeter with a survey rod at one-quarter intervals across width transects.

The water surface grade of each reach was determined from distance between points at the mid-stream depth locations using an engineering auto-level and standard levelling techniques. Gradients of each reach and/or potential electrofishing site (a reach or combination of consecutive sections of a reach) were weighted according to the area of each contributing section (ecological unit). Areas and gradients for use in population estimates were calculated by omitting sections with grades greater than 5%, i.e., white water chutes and falls. Reaches greater than about 1,000 m were sub-sampled to obtain a grade for comparison to the map grade.

Surveys were conducted once at each selected reach during 1984, 1985 or 1986. New reaches were added and others dropped in an attempt to distribute sampling with respect to the proportions of area by distance and gradient for entire river systems.

Electrofishing

Areas of electrofishing sites were limited in size to allow a single day for marking and single day for re-capture. An electrofishing site consisted of a single reach or consecutive sections of a reach totalling approximately 100 m of stream length. The cumulative length of consecutive electrofishing sites equalled the reach length if the area was small enough. Larger reaches were divided into smaller sub-reaches for electrofishing.

Electrofishing equipment consisted of a shore-mounted, generator-driven transformer, single anode, dip nets (2 max) and lipseine (Elson 1962). The four-person crew fished in a stream bank-to-bank pattern from bottom to top of the section. Locations in the main river where wading was not possible were fished with a generator-driven, double-boom, 4.9 m electrofishing boat[2].

Fish captured in a site were removed and held in an in-stream flow-through holding box for wadable sites, and in an on-board live box for electro-boat sites, until the site was fished over once. Fish were anaesthetized (MS222) and those larger than 5.0 cm were marked by squaring the tip of either the upper or lower caudal, right or left ventral, or anal fin. Fish were allowed to recover from the effects of the anaesthetic in a separate compartment of the holding box and were then dispersed throughout the site. Population estimates for sub-reaches were made possible by differential fin-clipping. One to three days generally passed between marking and sampling runs.

All fish larger than 5.0 cm were measured to a 0.5 cm fork length interval. Scale sampling proportionate to length-frequency classes enabled ageing by scale reading and therefore population estimates by age-classes.

Adjusted Petersen population estimates (Ricker 1975) for each site were calculated from mark-recapture data; known mortalities were added to the estimates. Minimum population estimates for sites with zero recaptures of marked fish were derived from the total catch. A Schnabel multiple mark-recapture estimate was calculated for one electro-boat site where two days of recapture effort occurred.

Electrofishing data were collected for the Stewiacke River, 1984 to 1988, and from the Saint Mary's River, 1985 and 1986, and are reported by Amiro et al. (1989). Additional data, including the Musquodoboit River, were collected in 1988 to 1990.

Modelling

Estimates of combined age-1+ and -2+ parr (herein referred to as total parr) populations were derived by four methods:

1) (MEAN) The product of the entire water surface area of the sampled river and the annual total parr arithmetic mean of the log-transformed densities. Confidence limits of the estimates were derived from estimates of the standard error of the means, the appropriate Student T value for the sample size and back-transformation.

2) (PDF) The most probable density and the 10 and 90% probability level densities were estimated

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[2] Smith-Root GPP 3.5, Smith-Root Inc., Vancouver, Washington.

from the data at median gradient values of the eleven gradient categories. Population estimates were derived from the area and the density estimates for each gradient category.

3 and 4) Parameters for two functional models, exponential (EXP) and quadratic (QUAD), were estimated from the data, and population estimates for each reach were derived from the reach area and gradient. Stream gradients were estimated from the map gradient of the reach. Confidence limits of predicted values for quadratic models were estimated from the standard error of the estimate using the $(X'X)^{-1}$ matrix (Snedecor and Cochran 1987). Suitable confidence limits for predicted values of exponential models are not available.

Definition of appropriate linearized models was restricted to the three principal metric variables, total parr density, site grade (area-weighted stream grade) and distance above the approximate head of tide (i.e., to the closest contour). Two categorical variables, year and tributary number were also examined for use in ANCOVA and post-hypothesis comparisons.

Variable selection in linear modelling for data from all years for each river proceeded by reducing the set of the three metric variables, squared metric variables and their interactions based on maximum R^2 and minimum multicollinearity or variable cross-correlation. The starting form of linear models was:

$$\text{ModelLn(Totalparr+1)=Constant+}$$

Exponential models were calculated with the same variables and with a constant for direct comparison to quadratic models. Exponential models without constants were estimated during calibration when non-significant constants were encountered or for derivation of some population estimates.

Data were processed and regression analysis was conducted by MGLH and NONLIN modules of SYSTAT[3]. Probability density estimates were derived from probability density function (PDF) smoothing parameters determined from algorithms and programming provided by D. Noakes as reported in Noakes (1989). Box plots were constructed according to the procedures of McGill, Tukey and Larson in SYGRAPH (Wilkinson 1990).

Calibrations

Independent estimates of the total parr population of the sampled rivers are not available. Counts of seaward-migrating smolts at Little River, a tributary of Stewiacke River, were obtained at a complete barrier fence and migration trap operated in 1990 and 1991. Estimates of a previous summer's total parr count was made for comparison purposes by dividing the smolt count by 0.25. This figure is within the range of possible values for the products of all age, sex and survival proportions for an Atlantic salmon stock with predominantly 2-year smolts (Elson 1967, 1975).

Annual total parr population estimates and projected smolt runs for Little River for 1989 and 1990 were derived by six methods:

1) (LR MEAN) The product of the mean (Ln transformed) density of Little River electrofishing sites and the area of Little River (1,473 * 10^2 m^2).

2) (RIV MEAN) Because the number of sites within a tributary is generally limited, the results obtained by using all electrofishing sites in the Stewiacke River was examined. The product of the mean density of all sites in Stewiacke River and the Little River area.

3) (PDF) The sum of products of the total area of each gradient category and the most probable density of each category.

4, 5 and 6) Because of the limited number of sites within the Little River parameters of exponential models, with (CEXP) and without (EXP) a constant, and a quadratic (QUAD) model derived from electrofishing data for the entire Stewiacke River were applied to the gradient and area values for each reach of Little River to estimate a density and population on a reach basis and for the entire Little River.

Bias and accuracy of annual estimated parr populations from each model for the entire Stewiacke River were assessed by correlating total parr populations with an index of egg deposition (Amiro and McNeil 1986) two years previous. Response of models to differences in habitat composition among rivers and the accuracy of the total population estimates were assessed by comparing the average recorded grilse catches to estimates of potential grilse catches for each river. Potential catches were derived from the average of annual estimates of the total parr populations for each model assuming 25% of the parr population became smolts, marine survival of 5.0% (close to the mean for Big Salmon River smolts reported by Jessop (1986) and Ritter (1989)) and angling exploitation of 33% (a value similar to those determined in the LaHave River by Cutting (1987)).

Results

Surveys

The aerial photo and orthophotographic map survey identified 301 reaches in 49 tributaries totalling 444 km of the Stewiacke River, 207 reaches in 29 tributaries totalling 295 km of the Musquodoboit River and 514 reaches in 47 tributaries totalling 586 km of the St. Mary's River. On-site stream surveys were conducted at 34 locations in 19 tributaries of the Stewiacke River, 22 locations in 15 tributaries of the Musquodoboit River and 24 locations in 16 tributaries of the St. Mary's River.

Factors used to adjust air-photo measured widths to mean summer low widths, averaged 1.071 and ranged from 0.81 to 1.23. Adjusted widths together with map-measured lengths were used to calculate

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[3] SYSTAT: The system for Statistics. Evanston, IL., USA.

water surface areas. Photographic interpretation problems, such as sun glint and shadow and vegetation canopy, reduced the number of comparable i.e., complete set of, width measurements, photo- and stream-measured areas to 12 locations on the Stewiacke river and 15 locations on the Musquodoboit (Fig. 2). St. Mary's data were not included in this analysis.

Accuracy and precision of map and photo-measured areas were checked by regression analysis of map and photo-measured areas with in-stream measured areas at selected reaches on both the Stewaicke and Musquodoboit rivers. Significant positive intercepts indicated a possible under-estimation bias in photo-measured areas. Slopes of the regression lines were 1.11 for the Stewiacke data and 0.80 for the Musquodoboit data indicating a slight over-estimation bias for the Stewiacke and an under-estimation bias for the Musquodoboit. The standard error of the estimate was 86.9 m^2 for the Stewiacke River and 98.5 m^2 for the Musquodoboit River. Because the slopes were near unity and because the constants not large, no adjustments were made to areas derived from air photos and maps.

Stream gradient (area-weighted percent) was compared to map-measured gradient at 55 locations on the Stewiacke River and 18 locations on the Musquodoboit River (Fig. 3). Unlike area comparisons, gradients could be obtained for all selected reaches. Stream gradient data were not angular transformed because, although theoretically bounded by zero, gradients are

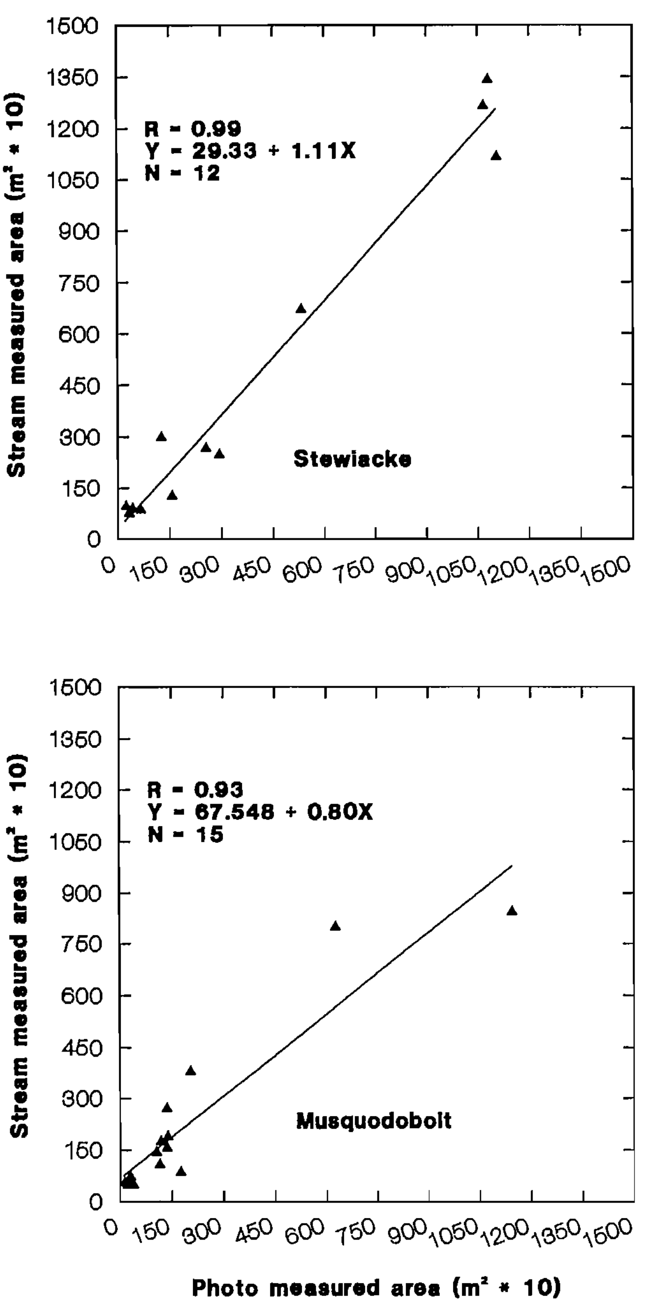

FIG. 2. Comparison of stream areas measured from aerial photography and from stream surveys for 12 sites on the Stewiacke River and 15 sites on the Musquodoboit River.

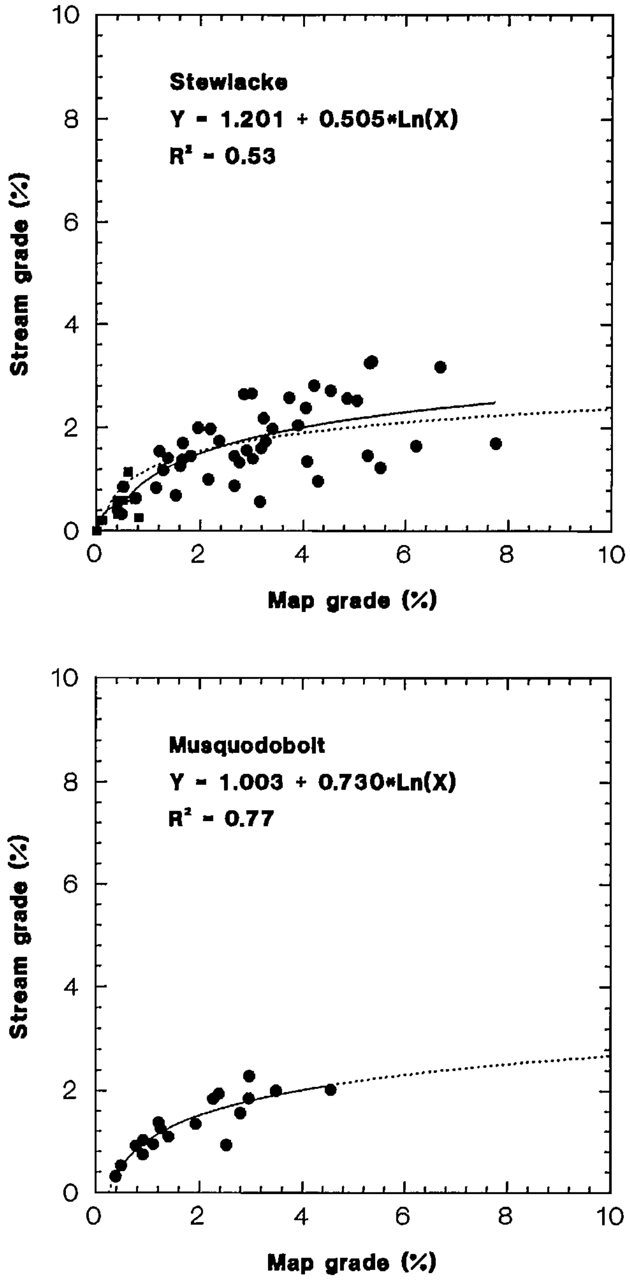

FIG. 3. Comparison of gradients measured from orthophoto maps and from stream surveys at 55 locations on the Stewiacke River and 18 locations on the Musquodoboit River. Dotted lines were derived from all reaches and solid lines from partial (■) and complete (•) surveyed reaches seperately.

not bounded at 100 as are percentages. In each case, natural logarithm (Ln) transformation of the map gradient was required to distribute the variance equally. Regressions were significant for each river but the variation accounted for was low ($R^2 = 0.53$) with a standard error of 0.59 (area-weighted surface grade) for the Stewiacke data but higher for the Musquodoboit data ($R^2 = 0.77$) with a standard error of 0.27. Slopes of regression lines for each river were not significantly different ($p = 0.26$) and parameter values were similar. Because the Stewiacke data were more extensive and available earlier in the project, those parameters were used in all subsequent calculations when map-measured reach gradients were converted to stream gradients. Equation 1 was:

Stream gradient=1.201+0.505*Ln(Map gradient)

Map grades less than 0.11% convert to stream gradients less than zero by this equation and therefore had to be assigned a value of zero for use in population estimation.

Total water surface areas, excluding lakes, estimated from maps and air photos were 27,000 * 10^2 m^2 for the Stewiacke River, 23,125 * 10^2 m^2 for the Musquodoboit River and 58,717 * 10^2 m^2 for the St. Mary's River. Distribution of stream surface areas by map grade category were similar for the Stewiacke River where 52% and Musquodoboit River where 65% of the surface area was in category 1 (Fig. 4). Only 32% of the St. Mary's River stream surface area was in category 1 and 42% was in category 2.

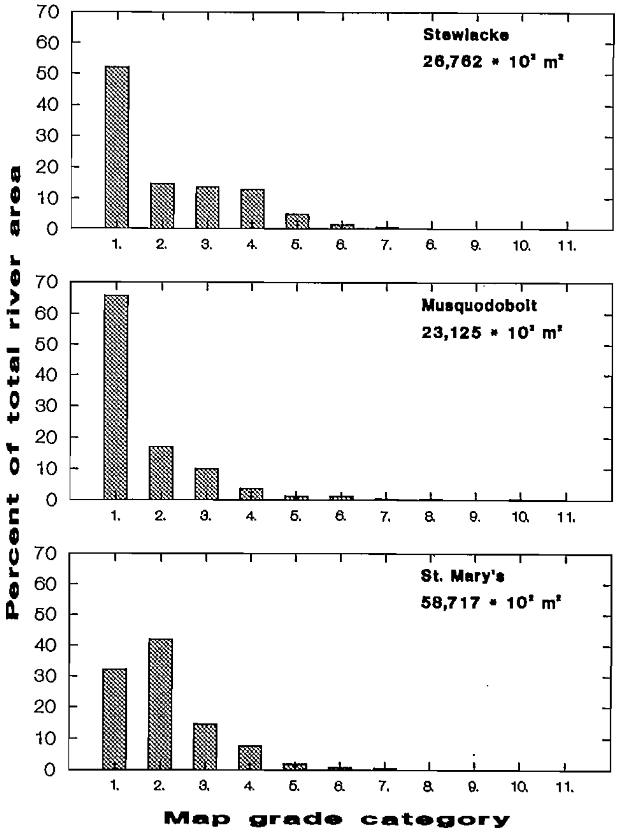

FIG. 4. Total surface areas of streams of the Stewiacke, Musquodoboit and St. Mary's river drainages measured from aerial photographs and categorized by map gradient.

Electrofishing

Population estimates of parr were conducted in portions of reaches termed "sites" during 1984 to 1990 in the Stewiacke River, 1988 to 1990 in the Musquodoboit River and 1985 and 1986 in the St. Mary's River. The number of sites varied annually from 29 to 44 in the Stewiacke River, 11 to 25 in the Musquodoboit River and 28 to 36 in the St. Mary's River. Reaches were randomly selected according to stream grade to proportionally represent the habitat distribution of the entire river. In spite of the use of light-weight electrofishing gear and an electrofishing boat, proportional distributions of sampling areas by gradient did not exactly match those of the entire rivers. The lower reaches of the main rivers, where gradients are generally lowest and areas largest, were difficult to sample reliably or consistently due to low water conditions which restricted operation of the boat between pools or stillwaters.

Five selected reaches, void of parr, were eliminated from further annual fishing efforts and from this analysis because of the uncertainties associated with recruitment due to access, droughts and unknown removals of adult fish from the streams. In the few cases where parr were not found, but gradients were favourable, fixed or temporary barriers were found down-stream of the sites or complete de-watering of the tributary was noted in drought conditions.

Electrofishing sites were distributed over 19 tributaries of the Stewiacke River, 15 tributaries of the Musquodoboit River and 16 tributaries of the St. Mary's River. No trend was noted in the gradients of sites sampled in up-river tributaries compared to those sites sampled in down-river tributaries. Annual densities (100^{-1} m^2) of total parr varied considerably. Arithmetic means were high in the Stewiacke River (39.2–23.1), lower in the Musquodoboit River (30.9–13.5) and lowest in the St. Mary's River (8.1–6.6). The effect of skewed distributions can be seen in a plot of the annual medians, 50 and 75% hinges and outliers (Box plots) (Fig. 5). Outliers of twice the hinge values effectively increase the arithmetic mean value but do not represent central tendency to the mean of the population sampled. Median values by these Box plots were more in the range of 20 total parr 100^{-1} m^2 for the Stewiacke and Musquodoboit rivers and 6 total parr for the St. Mary's River. Cumulative probability plots of total parr densities (Fig. 6) indicated transformation of the data was necessary before the assumptions to analysis of variance based on normal distribution could be made. A constant value of one was added to the total parr densities to allow transformation of zero values and provide all positive values.

Densities of total parr increased with stream gradient and maximal values occurred in map gradient class 5 in each river (Fig. 7). With the exception of St. Mary's River, parr densities declined in categories 6–8. Little or no area was defined in categories 8 to 11 in these rivers (Fig. 4).

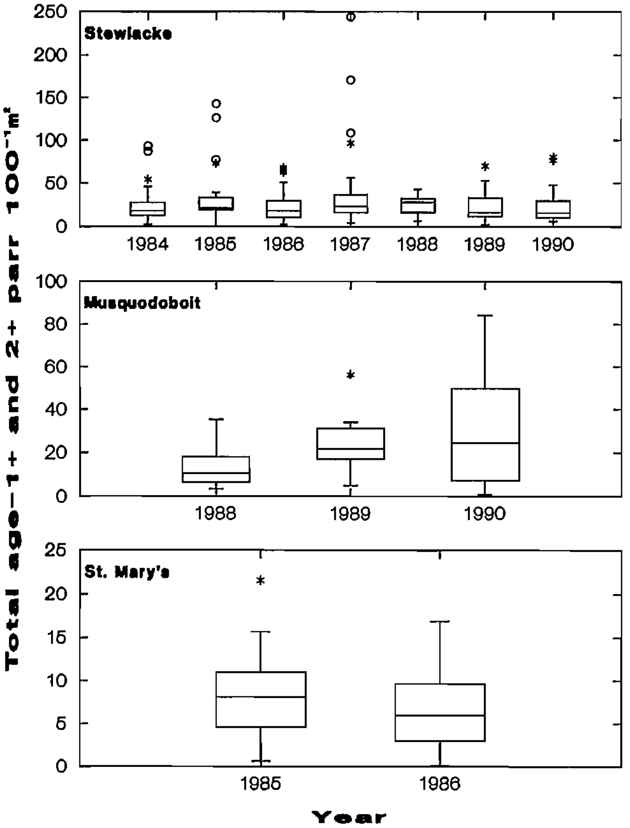

FIG. 5. Box plots of annual densities of total Atlantic salmon parr determined by electrofishing the Stewiacke, Musquodoboit and St. Mary's rivers. Plots show the median, 25% hinges and outliers (*) and 75% hinges and outliers (O).

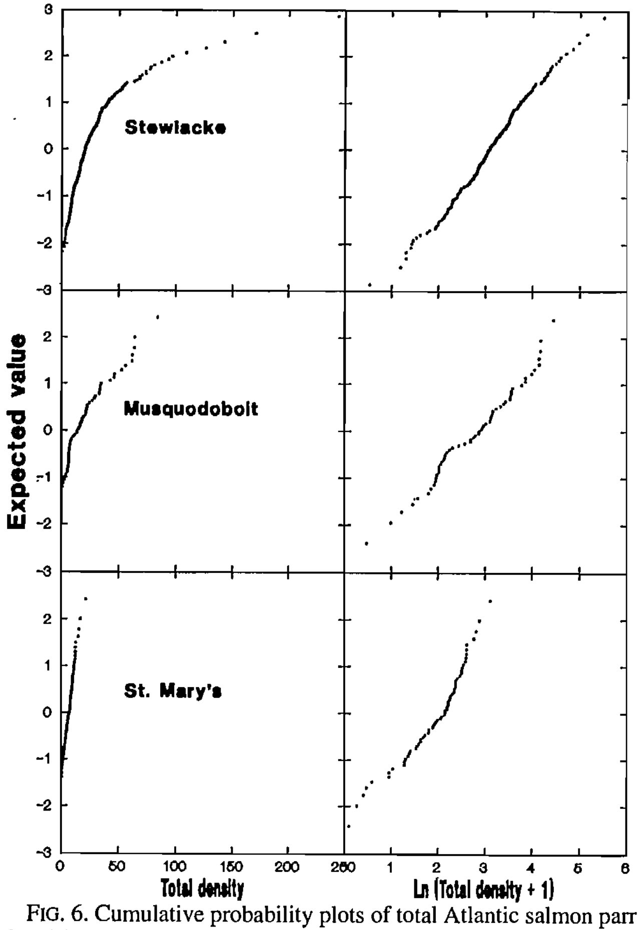

FIG. 6. Cumulative probability plots of total Atlantic salmon parr densities for raw and Ln transformed data for three rivers.

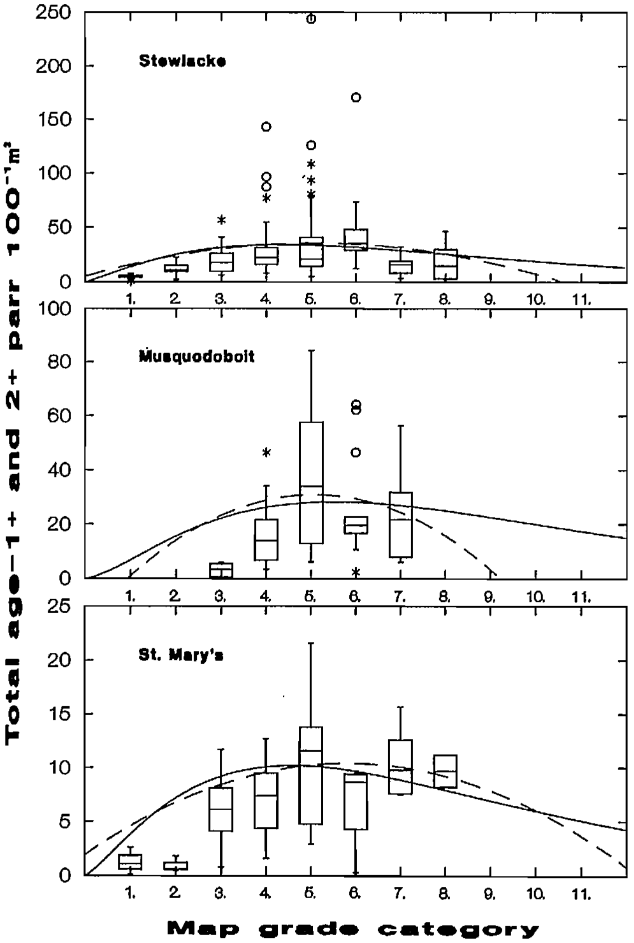

FIG. 7. Box plots of total Atlantic salmon parr by map gradient categories for the Stewiacke, Musquodoboit and St. Mary's rivers. Broken line shows a fitted quadratic curve and solid line shows a fitted negative exponential curve.

The consistency of gradient as an indicator of habitat preference was observed at three locations with seven sites fished from 1985 to 1990 in the Little River, Stewiacke. Sites with stream gradients between 0.6% (category 3) and 1.2% (category 5) had consistently higher parr densities than lower or higher gradients (Fig. 8). Lower parr densities found in the higher gradient sites may have been due to the distance from the confluence with the main river up-stream to the site but the data were not sufficient to adequately address this question.

Model Development

General linear models

Plots of parr densities by stream grade or gradient categories indicated a dome-shaped relationship in all but the St. Mary's River. Densities in the St. Mary's were, however, two to three times less than those observed in the Stewiacke and Musquodoboit. This observation could imply that densities in preferred habitats (grade categories 3–6) were restricted by factors like recruitment that are extrinsic to the model. Also, the limited number of sites with high grades, if selected for sampling, were

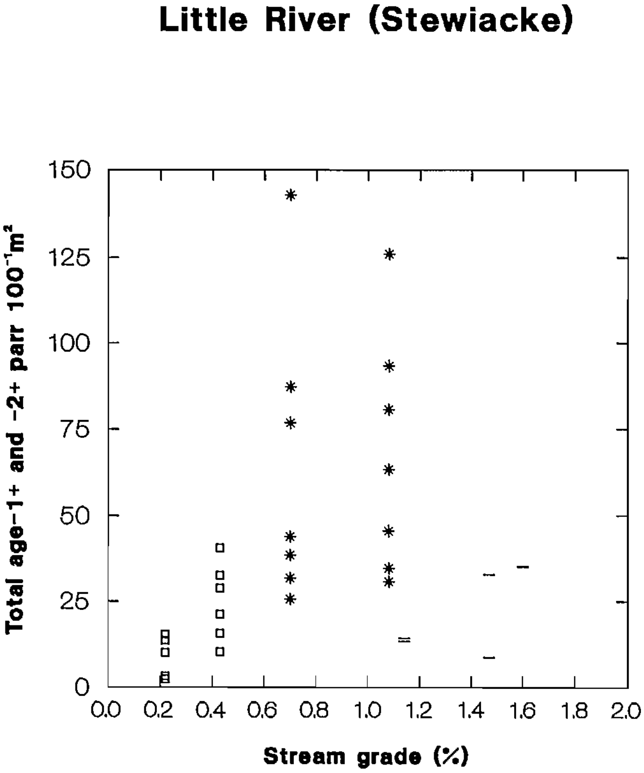

FIG. 8. Annual total Atlantic salmon parr densities determined by electrofishing at seven sites at three locations (symbols) in Little River, a tributary of the Stewiacke River, 1984 to 1990.

sometimes void of parr. If no parr were found, then these sites were reviewed for possible elimination depending on the presence of parr above the site.

When the variable Grade was added, only the St. Mary's River had a statistically significant probability of <0.01, but only 15% of the variance was explained (Table 1.). The addition of Grade^2 to the model (a parameter responsible for the domed shape) resulted in significant models for all three rivers and the portion of the explained variance ranged from 17 to 27%. Constants were always positive but not significant (p=0.14) in the Musquodoboit data. The addition of Distance to the model resulted in significant models for all rivers and the portion of the variance explained by the models ranged from 23 to 38%. The constant was not significant at p=0.22 in the Musquodoboit data set and the Distance term was not significant at p=0.94 for the St. Mary's River data set. Additional interaction terms did not appreciably increase the R^2 and/or pass tolerance for multicollinearity and therefore were not included in further analysis.

Analysis of co-variance

General linear models were fitted to data from all years despite the possibility of wide ranges in annual recruitment and in survival values within the main river and among tributaries. Despite these encumbrances the models explained a respectable amount of variability in total parr densities with Grade and Distance. Analysis of co-variance (ANCOVA) for the categories (effects) Year and Tributary was used to examine their effect in improving the total explained variance.

The first ANCOVA model tested the Year effect and included Grade and Grade^2 for the St. Mary's River data plus Distance for the Stewiacke and Musquodoboit rivers' data (Table 1.). Year as a categorical variable was not significant at the p=0.01 level of probability in any river, however, it was significant at the p=0.05 level in the Musquodoboit and St. Mary's rivers. The R^2 values ranged from 0.32 to 0.49.

The second ANCOVA model tested the Tributary effect and only included Grade and Grade^2 in all three rivers because of the high correlation between Tributary number and Distance. Tributary as a categorical variable was significant at p<0.01 for the Stewiacke, p=0.03 for the Musquodoboit and p=0.02 for the St. Mary's. The R^2 values ranged from 0.55 to 0.67. The Grade^2 variable dropped in significance to p=0.03 for the Musquodoboit River data.

The combined effects of Year and Tributary were examined in a third ANCOVA model containing Grade and Grade^2. In each river all metric and categorical variables were significant at p<0.05 or lower and the models explained 59 to 73% of the variance in total parr densities.

Year effect was not significant without the inclusion of grade in any river analysis. However, Tributary effect was significant at p<0.05 or less in each river for all years. Analysis of variance with Year and Tributary effects together indicated significant Year effect in the Stewiacke, accounting for 52% of the variance, but not in the Musquodoboit or St. Mary's rivers' data.

Non-Linear Models

The virtual absence of parr in larger, essentially zero-grade, reaches and the rapidly increasing occurrence of parr in faster-flowing, i.e., increasing gradient, reaches combined with the tapering off of densities at higher stream gradients, suggested a nonlinear model would better represent the response of parr density to stream gradient. A non-linear model representing exponential growth and decay used in epidemiology in the form:

$$Y+A*X^{B*EXP(-X)}$$

has a response curve of this shape. The addition of a distance parameter (+C*Distance) raises or lowers the curve in the third dimension, if required.

This exponential model, with Ln (density total parr + 1) and Grade as the dependent and independent variables, was parameterized for the complete Stewiacke River data set. When both models included a Constant and a Distance variable, the raw R^2 was 0.964 for the negative exponential model compared to 0.942 for the quadratic model.

TABLE 1. Correlation coefficients, and null hypothesis probabilities greater than 0.01 of regressions and variables used in general linear model development of total Atlantic salmon parr in the Stewiacke, Musquodoboit and St. Mary's rivers.

River Model Ln(Totparr+1)=Constant +	R^2	Probabilities > 0.01 Rgn.	 Const.	 Grd.	 Grd.^{2}	 Dist or Trib	 Year
Stewiacke River N = 236; Tribs = 19; Years = 7							
Grade	0.01	0.11		0.11	—	—	—
Grade + Grade^2	0.17					—	—
Grade + Grade^2 + Distance	0.33						—
Grade + Grade^2 + Distance + Year$	0.37	—	—				0.08
Grade + Grade^2 + Tributary$	0.55	—	—				
Grade + Grade^2 + Tributary$ + Years$	0.59	—	—				
Musquodoboit River N = 59; Tribs = 15; Years = 3							
Grade	0.14				—	—	—
Grade + Grade^2	0.27		0.14			—	—
Grade + Grade^2 + Distance	0.38		0.22				—
Grade + Grade^2 + Distance + Year$	0.49	—	—				0.02
Grade + Grade^2 + Tributary$	0.67	—	—			0.03	—
Grade + Grade^2 + Tributary$ + Year$	0.73	—	—	0.09	0.10		0.03
St. Mary's River N = 64; Tribs = 16; Years = 2							
Grade	0.15				—	—	—
Grade + Grade^2	0.25					—	—
Grade + Grade^2 + Distance	0.23					0.94	—
Grade + Grade^2 + Year$	0.32	—	—			—	0.05
Grade + Grade^2 + Tributary$	0.57	—	—		0.03	0.02	—
Grade + Grade^2 + Tributary$ + Year$	0.61	—	—		0.02	0.02	0.05

($indicates a categorical variable; — indicates test not applicable.)

This comparison indicated that little statistical improvement would be expected for the exponential model. However, because predicted values from exponential models at the lowest and highest gradient reaches (Fig. 7) can be quite different than quadratic models, and, because extensive areas of low gradient are found in the sampled rivers, population estimates derived from exponential models were examined.

Annual Models

Parameters for both exponential and best-fit quadratic models were estimated for each year and river. Analysis began using quadratic models which included a Constant, Grade, Grade^2 and Distance. Examination of parameter fit and condition indices, to test for variable inter-correlation, guided the inclusion or rejection of parameters to both the quadratic and exponential models. Parameters for an exponential model without a Constant were also derived in order to examine the effect of a constant on the output of the models when applied to the entire river areas.

In the Stewiacke analysis, regressions were significant (p<0.02) in all years. The Grade^2 parameter fit was not significant in 1987 (p=0.09) and 1988 (p=0.24). The Grade parameter fit was not significant (p=0.13) in 1988. Multiple R^2 for quadratic models and corrected R^2 for non-linear fits involving a constant were similar and ranged from 0.27 in 1987 to 0.68 in 1985. Residual mean square error was consistently greater for exponential models without a Constant and was consistently less for quadratic models.

In the Musquodoboit analysis, regression was significant (p<0.01) in 1989 and 1990 but not significant (p=0.18) in 1988. Parameters were generally more poorly fitted compared to the other rivers and in 1989 neither the Constant (p=0.60) nor the Grade (p=0.25) were fitted significantly. However, when regression was significant, R^2 values were 0.83 in 1989 and 0.61 in 1990 for both model forms.

In the St. Mary's analysis, regressions were significant (p<0.02) in both years. The Distance parameter was not significant (p=0.74, 0.68) in either 1985 or 1986. Grade^2 was not significant in 1985 with (p=0.18) or without (p=0.17) the Distance variable.

Annual estimates were therefore derived from models without a Distance variable. R^2 values ranged from 0.35 for the exponential model in 1986 to 0.33 for the quadratic model in 1985.

Total Population Models

Annual estimates of total parr, derived by four methods, varied considerably in magnitude, in precision and in accuracy when compared to a measured output of smolts or to observed angling catches when a smolt proportion and constant survival rate was applied to the estimates. An example of the tabular output (Table 2.) is shown for parameters derived from the combined 1984 to 1990 Stewiacke River data set using the quadratic model.

Annual estimates of total parr for the Stewiacke River ranged from a high of 617,089 parr (521,089–729,908, 90% CL) from the product of the mean and total area in 1988 to a low of 200,637 parr (133,588–329,106, 90% CL) from a quadratic model in 1989. Estimates for the Musquodoboit River ranged from a low of 76,508 parr (90% CL not available) from an exponential model in 1990 to a high of 455,977 parr (310,801–664,271, 90% CL) from the mean in 1989. Estimates for the St. Mary's River ranged from a low of 163,368 parr (90% CL not available) from a exponential model in 1986 to a high of 409,405 parr (329,521–505,726, 90% CL) from the mean in 1985.

Calibration to Counts

Counts of smolts out of Little River were 3,579 in 1990 and 3,144 in 1991. Water conditions were poor for smolt migration in 1991 and significant numbers of smoltified parr did not migrate out of Little River or out of adjacent non-barriered tributaries. If 25% of the population had smoltified and migrated, then the total parr population in Little River was 14,316 in 1989 and 12,576 in 1990. Estimates of the total parr population of Little River ranged from 15,437 by exponential model without a Constant (CEXP) to 47,101 total parr estimated from the 1990 Little River electrofishing sites (LR MEAN), (Fig. 9).

The two-year combined result from exponential (EXP) models without a Constant was 18% higher than the two-year combined estimated smolt run. The PDF approach was 26% higher than the combined count. Quadratic (QUAD) and exponential models with a Constant (CEXP) were almost equal and about 83% higher than the combined counts. The Stewiacke River mean (RIV MEAN) was 2.11 times or 111% higher than the combined count. The Little River mean (LR MEAN) was 2.75 times the combined count.

To further assess performance, distribution of area by gradient category was compared to the distribution of fish produced by gradient category for the Little River (Fig. 10). The greatest difference between area distribution and fish distribution was in the lowest gradient category. In the first category all models produced less than one smolt 100^{-1} m^2 with the least number coming from the EXP model without a Constant and the largest estimate from the QUAD model. Category two, the most abundant area of the tributary, was the dominant production category of the PDF and QUAD models but not of the non-Constant EXP model. The remaining categories produced proportional to their areas for all models except EXP where production increased with each category to the fourth category.

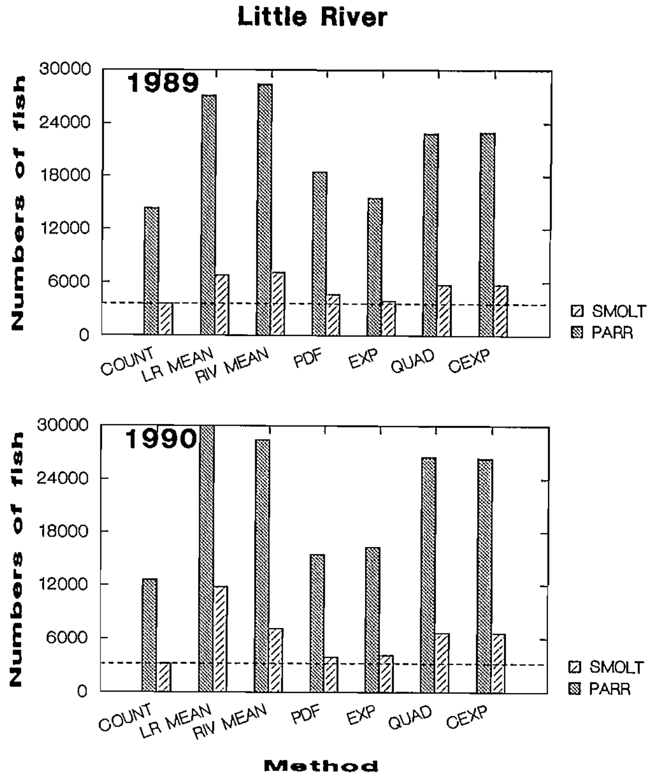

FIG. 9. Comparison of counted and estimated smolts and total Atlantic salmon parr in Little River, a tributary of the Stewiacke River, 1989 and 1990. Techniques were; COUNT is the Little River trap count of smolts and estimated parr; LR MEAN is derived from Little River electrofishing sites; RIV MEAN is derived from all Stewiacke River electrofishing sites; estimates of total parr for Little River were derived by four statistical models based on electrofishing in Stewiacke River; PDF is a probability density function; EXP a negative exponential function; QUAD a quadratic function; CEXP a negative exponential function with a constant.

Calibration to Indices

The ability of the models to index past escapement was examined by correlation to an index egg deposition for the Stewiacke River (Fig. 11). The highest R^2 was with the MEAN ($R^2 = 0.89$) followed closely by the EXP model ($R^2 = 0.86$). The worst index was the PDF model ($R^2 = 0.13$). The QUAD or CEXP models were intermediate ($R^2 = 0.37$).

The ability of the models to account for variation in production among rivers of different habitat distributions was examined by forecasting grilse harvests from potential smolt runs averaged for the years of

TABLE 2. Stream areas (100 m^2) (upper figures) by stream gradient (%) and distance (km) categories and numbers of Atlantic salmon parr (lower figures) derived from a quadratic model fitted using the combined 1984 to 1990 electrofishing densities for the Stewiacke River, with total area and parr population, percent contribution to parr and stream area and average densities 100^{-1} m^2 of gradient and distance categories. Model parameters and 90% confidence limits of the total parr population estimate are given below.

	Gradient													
Distance	0–0.12	0.121–0.249	0.25–0.49	0.5–99	1–1.49	1.5–1.99	2–2.49	2.5–2.99	3–3.49	3.5–5.0	>5.0	Totals	Percent	Density
00–10	3,000	116	142	0	0	0	0	0	0	0	0	3,258	12.1	
	444	1,887	5,482	0	0	0	0	0	0	0	0	7,813	3.1	2.40
10.001–20	3,238	668	63	29	6	0	0	1	0	0	0	4,007	14.8	
	2,555	9,718	2,069	1,341	314	20	0	74	0	0	0	16,091	6.5	4.02
20.001–30	2,824	86	244	419	21	16	2	3	0	0	0	3,616	13.4	
	639	1,659	6,935	14,925	870	667	106	132	0	0	0	25,932	10.4	7.17
30.001–40	2,865	0	264	732	157	29	0	0	0	0	0	4,047	15.0	
	936	0	5,803	24,072	5,884	1,157	0	0	0	0	0	37,852	15.2	9.35
40.001–50	1,972	1,557	411	175	33	8	6	0	5	2	0	4,170	15.4	
	1,122	12,929	7,312	4,680	1,044	255	212	0	146	58	0	27,757	11.1	6.66
50.001–60	28	1,480	1,390	702	288	55	33	7	4	6	0	3,994	14.8	
	0	14,372	22,899	15,062	7,504	1,491	837	173	97	138	0	62,572	25.1	15.67
60.001–70	0	0	1,046	1,092	510	166	88	21	20	7	5	2,954	10.9	
	0	0	15,417	20,633	11,427	3,851	2,007	462	446	141	81	54,466	21.9	18.44
70.001–80	0	0	80	267	235	91	0	0	0	0	0	703	2.6	
	0	0	1,119	4,589	5,209	1,828	0	0	0	0	0	12,744	5.1	18.13
80.001–90	0	0	0	14	166	72	0	0	0	0	0	252	0.9	
	0	0	0	200	2,628	1,163	0	0	0	0	0	3,992	1.6	15.85
Total area	13,928	3,907	3,640	3,430	1,445	438	130	32	29	16	5	27,000	100.0	
Total parr	5,695	40,564	67,035	85,502	34,880	10,432	3,163	841	689	337	81	249,218	100.0	9.23
Percent area	51.6	14.5	13.5	12.7	5.4	1.6	0.5	0.1	0.1	0.1	0.0			
Percent parr	2.3	16.3	26.9	34.3	14.0	4.2	1.3	0.3	0.3	0.1	0.0			
Parr 100^{-1}m^2	0.41	10.38	18.41	24.93	24.13	23.83	24.26	26.04	24.00	21.54	17.53			

Model: Ln(Y) = C + B1*X + B2*X(1)^2+ B3*X(2); X(1) = Area Wt'd Surface Grade; X(2) = Distance km/100; Y = Ln(Total Parr + 1) 100 $^{-1}$*m^2; C=2.69; B(1) = 2.08; B(2) = −0.72; B(3) = −1.58 90% Confidence interval: (213,527–293,703).

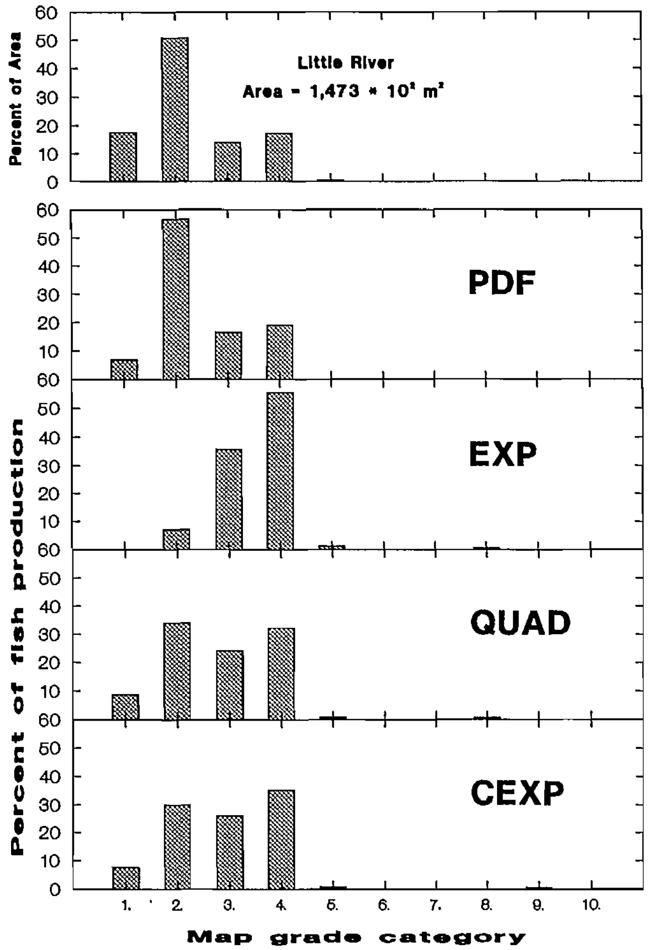

FIG. 10. Distribution of area and population of total Atlantic salmon parr by map gradient for four methods for Little River, tributary to Stewiacke River.

record. Potential harvests derived from the MEAN model were always the largest forecast and greater than recent average annual catches in any river (Fig. 12). Stewiacke River forecasts were all greater than the recent mean catch of 850 grilse. Potential catches ranged from 21% to 61% higher than the average catch by functional models, 99% higher by the PDF and 270% higher by the MEAN. Potential catches for the Musquodoboit were close to the average catch of 366 grilse for CEXP (10% higher), EXP (25% higher) and QUOD (11% lower) and higher for the PDF (52%) and MEAN (403%). St. Mary's River forecasts were less than the average of 1,234 grilse for all models other than the MEAN. In general, models except the MEAN, PDF and CEXP, forecast catches from −11% to +40% of the observed catches without further tuning with annual or river-specific survival rates to the one sea-winter stage.

Discussion

Habitat measurement

Total water surface area for the Stewiacke River was estimated to be 27,000 * 10^2 m^2 or 36% greater than the reported accessible rearing area (Anon. 1978). Similar disparities were found for the Musquodoboit

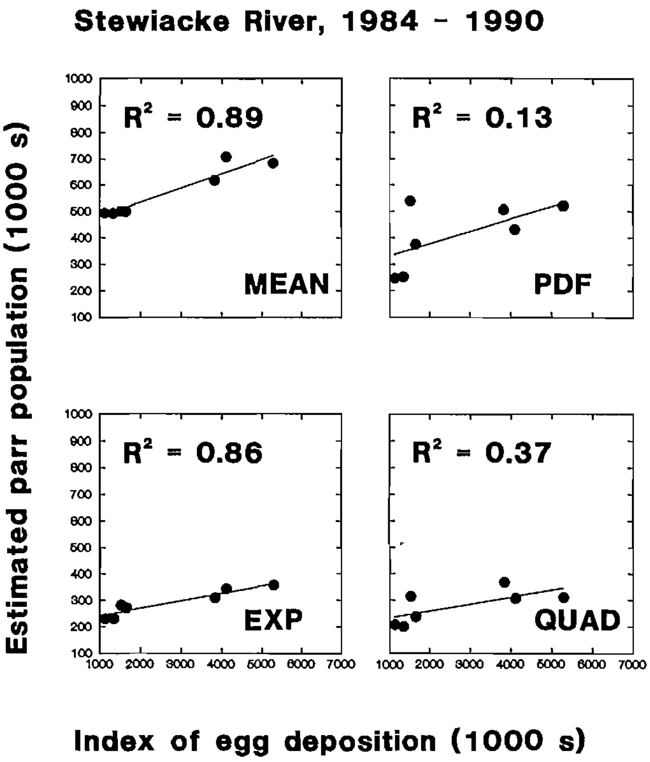

FIG. 11. Correlations between estimated total Atlantic salmon parr by four estimation techniques and index of egg depositions for the Stewiacke River, 1984 to 1990. Techniques were; MEAN of electrofishing sites; PDF probability density function model; EXP negative exponential function; QUAD quadratic function.

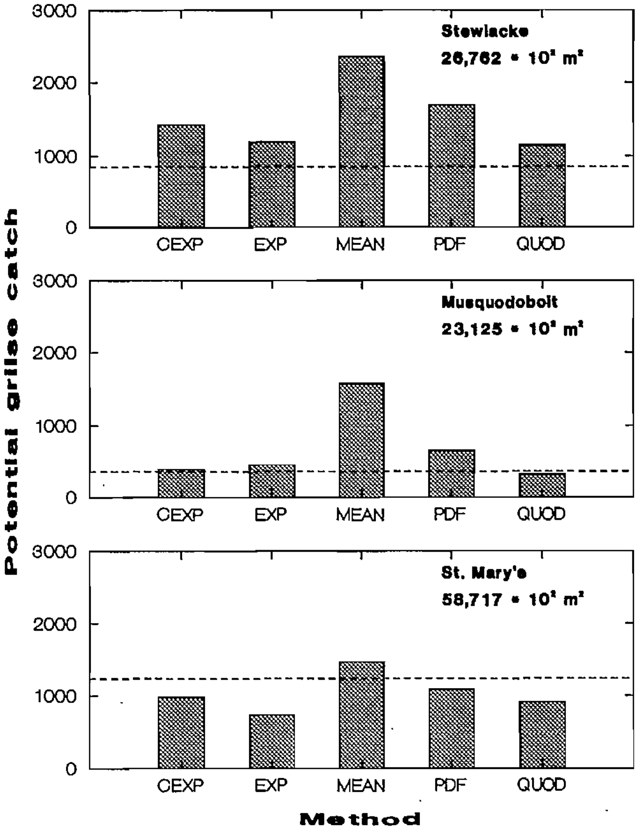

FIG. 12. Estimated potential one-sea-winter (grilse) catches from total Atlantic salmon parr population estimates and constant survival rate for the Stewiacke, Musquodoboit and St. Mary's rivers. Dashed line indicates the average reported grilse catches.

River where the estimate was 56% greater and for the St. Mary's River where the estimate was 48% greater. These increases may be attributable to exclusion of low gradient areas and incomplete inclusion of all tributaries in the 1978 estimates. Area less than 0.12% map grade comprised 52% of the total water surface area of the Stewiacke and provided 0 to 42% of parr production, depending on the parr model used, indicating the importance of accurate accounting of production in low gradient reaches. Existing production models rely on subjective inclusion of habitat and constant rate of production throughout a drainage basin and therefore are subject to large potential error.

Because the more-accurate models examined here did not result in high numbers of parr in low gradient areas and because area greater than 0.12% gradient was smaller than previous estimates, these current results may be regarded as minimum estimates of production area. Overhanging vegetation could account for the negative bias for remote- measured reaches. However, unlike other salmonids occupying cold streams, Atlantic salmon are for the most part photo-positive (Keenleyside and Yamamoto 1962; Gibson and Keenleyside 1966) and the unaccounted for area under overhanging cover may not contribute significantly to under-estimation of salmon production.

Use of low gradient habitat by Atlantic salmon parr was infrequent in the three rivers examined or in any tributary of those rivers. These results were consistent and occurred in tributaries with high densities. In low gradient reaches, parr occupied short higher gradient runs and riffles connecting still waters which are less frequent in the wider lowest gradient sections of streams. Because of low resolution, map and photo surveys cannot account for localized areas of producing habitat in low gradient reaches.

Lack of precision in the map-to-stream gradient conversion equation imposes a physical limitation on the resolution of map-based production models. Gradients estimated from contour lines may be imprecise because they are established from the surrounding terrain and not the water surface. Estimates of stream gradients established from terrain contours may not be precise enough to address reach-specific questions. Establishing elevations for the water surface of the streams would be more precise. Higher-resolution photographic interpretation techniques are available but at higher costs associated with custom photography and interpretation. If a habitat production issue relates to a specific reach, then an on-site stream survey is more economical and accurate.

Parr Distribution

Densities varied considerably but were higher at sites with moderate gradients. Category 5 (1.0 to 1.5%) had the highest median densities within each river and year. Densities greater than 50 parr were also encountered in category 4. These data support the hypothesis that stream gradient is a viable indicator of habitat use. Setting the upper limit of gradient suitability is difficult because of the zero density problem. However, data show that parr were not found higher than category 8 (2.501 to 3.0%). This finding is similar to observations by Elson (1975) and Mills (1973) although grades are measured differently here. It is clear from observation that salmon parr do not live in waterfalls and therefore an upper limit to occupation of stream habitat by parr based on grade must exist.

Objective evaluation of the hypothesis that Atlantic salmon parr are distributed with respect to stream gradient required that electrofishing sites with zero parr density, without known populations of parr upstream of the sites, had to be eliminated from the analysis. Zero densities could be associated with factors intrinsic to the hypothesis, i.e., poor habitat quality (too low or high stream gradient) or to extrinsic factors, i.e., low recruitment, water quality or other environmental factors. Some zero density observations would support while others would serve to reject or weaken the hypothesis. It is more likely that there is a stream gradient limit to habitat use by parr and that more extensive data and logistic modelling could establish the average upper limit.

Low resolution of models based on gradient alone is not surprising because of the inter-annual variation in escapement, survival to parr stages and under-distribution of spawners to all tributaries. However, habitat preference based on stream gradient can be inferred from the Little River data. Despite large differences in annual recruitment, more parr were consistently found in moderate gradient than in lower or higher gradient reaches. The inter-annual variation of parr densities at low gradient sites was much less than that at moderate gradient sites (Fig. 8).

The addition of distance as a second significant variable supports the hypothesis that the upper tributaries of these streams, though meeting the physical habitat criteria, are not preferred areas for Atlantic salmon. This observation supports a theory of habitat segregation between salmonids co-habitating coastal streams (Huet 1959; Jones 1975). Upper reaches are generally cooler because of greater stream cover, greater proportion of ground water and stepped gradient (higher pool area to riffle area ratio) because of the downstream distribution of smaller substrate materials. These features favour species such as brook charr (*Salvelinus fontinalis*) rather than Atlantic salmon. However, other factors, such as run timing and river morphology, may alter this segregation, and results like those found for the St. Mary's (non-significant Distance factor) may not be uncommon. River systems, like the St. Mary's, which have substantial lakes distributed along their courses provide extensive summer holding areas for adult salmon thereby reducing mortality of early-season river entry fish. Also substrate distribution in tributaries flowing into these lakes can be similar to main river courses without lakes and parr distribute in a similar fashion. Distance from the mouth of the main river would not be expected to simply account for parr distribution in these cases.

Analysis involving tributaries as categorical variables support a theory of stable sub-populations of salmon within rivers (Riddell and Leggett 1981; Shackley and Donaghy 1992). This implies that if data were sufficient to conduct a two-way ANOVA factored by tributary and year then residual error would be significantly reduced because variation in recruitment patterns among tributaries would be accounted. Population densities among tributaries may vary due to biological interaction with physical or chemical constraints which are beyond the basic habitat criteria examined here. ANOVA modelling was not pursued in this analysis because it requires more-intensive sampling. ANOVA modelling is well suited to post-hypothesis tests, especially in response to specific questions, but not to prediction and modelling.

Modelling

Counts of smolts, observations of parr during electrofishing and attempts to conduct estimates in low gradient sections of streams devoid of parr indicate that functional models without constants are less biased in estimating the total population of parr in the rivers sampled. A constant (intercept) is not likely to be significant if sufficient samples are drawn from low-gradient, sparsely populated areas. However, experimental objectivity, water depths, accessibility, and significant sample size for population estimation often restrict the availability of estimates in these areas. If sampling indicates that parr are not present in low gradient areas and population estimation, rather than statistical inference such as post-hypothesis contrasting, is the objective, then zero intercept models such as a quadratic forced through the origin or an exponential model without a constant, will yield output with less bias.

Negative exponential models without a constant display the best theoretical response to the observed distribution of parr. Densities can be zero at zero gradient by eliminating the constant, rise rapidly to a height set by the A parameter, and maximize quickly with increasing Grade at the point set by the B parameter. Unlike the quadratic model, the negative exponential model declines slowly allowing for production at higher gradient reaches similar to some of the observed data. A Distance variable and parameter merely gives a series of similar curves of differing heights for the given distance. This response, rapid rise in density with grade and slow decline to some theoretical maximum grade, best describes the observations and is recommended for estimation modelling and for use in habitat preference models. However, for statistical comparisons like post-hypothesis contrasting of years, reaches, and rivers, quadratic models are more useful to the practitioner because of their intrinsically linear nature which has application to a vast range of statistical procedures.

Because the grade conversion (Equation 1) results in negative site grades below 0.11 map grade values (which default to 0.0), there is some resistance to high population estimates in very low gradient reaches. This calibration step could underestimate populations in ponds or still waters if parr are found in measurable numbers in these habitats, such as occurs in Newfoundland (Pepper 1976).

Probability density models may be better or as well-suited to total population estimation if sample size is sufficient to allow stable estimates across all gradient classes. Sample sizes were barely sufficient to allow stable estimates for the one variable (Grade) and large confidence limits resulted. Three dimensional PDF models (incorporating Distance as the second co-variable) were not estimated because of the requirement for a minimum of 67 samples for stable (± 10%) parameter estimates (Silverman 1986).

Calibrations

Correlation between index egg depositions and population estimates derived from the mean parr density was higher because of the broader range in population estimates derived from means. Extremely high densities of parr at a few electrofishing sites, following high angling years, strongly contribute to the relationship but do not reflect overall total parr production in the rivers. This result infers that large numbers of returning salmon can be derived from relatively small sub-populations within a river or tributary.

Calibrations to indices of potential harvests for the three rivers demonstrate a valuable use for the models. Without attempting to adjust with annual and river-specific survival rates, function models forecast production of the rivers within 41% of observed catches. Models correctly accounted for the two-fold difference in water surface area and habitat distribution. Results for the St. Mary's river were somewhat suprising in that it has the greatest proportion of habitat with gradient >0.12% yet had the lowest parr densities. This analysis points to a serious production problem in the St. Mary's drainage. Additional ANCOVA analysis of the St. Mary's data may indicate whether tributaries, branches or the entire river contribute to the relatively low production. Further application of these modeling techniques may indicate areas for improvement in production of parr in the St. Mary's River.

The apparent higher-than-expected average angling catch of grilse in the St. Mary's River may be explained by the 5% smolt survival rate. Survival rates of Atlantic coast stocks are confounded by the proportion of a stock maturing and returning after one sea-winter. This proportion influences the survival rate because of the increased natural and fishing mortality associated with an additional year at sea.

Survival to home waters of Atlantic coast mixed age-at-maturity stocks may be twice that of inner Bay of Fundy stocks (Ritter 1989).

Other potentially valuable uses of the these modelling techniques are to estimate past spawning escapements and required spawning escapements. Estimating past escapements is a straight-forward correction for a known or best estimate of survival. Estimating required egg deposition requires an additional factor, a target, maximum or optimum total parr density. This level of parr must be selected through other factors and methods such as stock-recruitment, maximum biomass production, density-dependent growth or survival. Once the maximum parr density of preferred habitat is decided then a model can be calibrated, parameters derived and, through selected survival values, the required egg deposition can be calculated.

Distribution of age-0+ parr (fry) according to stream gradient has been inferred by Elson (1967) and others. Significant correlations for all linear and one quadratic relationship between density of age-0+ parr and stream gradient (measured as the difference in elevation over the site length) were reported by Kennedy and Strange (1982). Analysis of companion data for age-0+ parr densities in the Stewiacke, Musquodoboit and St. Mary's rivers (not presented) was similiar to the results reported here for age-1+ and -2+ parr. This corroborates the earlier research and with the gradient conversion equation reported here enables the generation of models of habitat use and distribution for all ages of Atlantic salmon parr.

The substantive gain in precision with the introduction of a tributary factor and the circumstantial evidence supporting the theory of stable subpopulations at the tributary level within rivers indicates a promising direction for future research. Establishing a cause or finding a signal for differing production levels between tributaries would substantially increase the accuracy and precision of the modelling technique for tributaries within a river system.

Habitat use, production and required egg deposition calculations for many rivers is an evolving requirement of Atlantic salmon management. While the desire to produce a precise high resolution production modelling technique remains, the requirement for a low resolution, broadly applicable technique within agency budgets is immediate. The data, analysis and hypotheses presented here attempt to integrate a collection of techniques from the sciences of remote sensing, hydrology and fisheries biology to provide economic and feasible scientific approaches to issues in the management of Atlantic salmon applicable over the wide geographic range of the species.

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Self-Thinning in Stream-Dwelling Salmonids

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I used data from four published studies to calculate self-thinning lines ($\log_{10}$ mean weight vs. $\log_{10}$ density) for stream-dwelling salmonid fishes. The slopes of these lines were compared to three hypothetical slopes: −1.00, which assumes the total biomass of the population remains constant during self-thinning; −1.08, which assumes territory size limits population density; and −1.33, which assumes the total metabolic rate of the population remains constant during self-thinning. Three of four studies were consistent with the constant-metabolic-rate line and did not support the other two hypotheses. This study provides some preliminary data to support a self-thinning line with a slope of −1.33 for stream-dwelling salmonids.

J'ai utilisé les données fournies par quatre études publiées pour calculer les courbes d'auto-éclaircie ($\log_{10}$ poids moyen c. $\log_{10}$ densité) pour les salmonidés de milieu lotique. Les pentes de ces courbes ont été comparées à trois pentes hypothétiques : −1,00, pour laquelle la biomasse totale de la population reste constante pendant l'auto-éclaircie; −1,08, pour laquelle la taille du territoire limite la densité de la population; enfin, −1,33, pour laquelle le métabolisme total de la population reste constant pendant l'auto-éclaircie. Trois des quatre études donnaient des résultats qui concordaient avec la courbe du métabolisme constant et ne confirmaient pas les deux autres hypothèses. Le présent travail offre des données provisoires qui confirment pour les salmonidés du milieu lotique une courbe d'auto-éclaircie à pente de −1,33.

Introduction

The population density of individuals within a cohort of fish decreases over time for a variety of reasons including predation, disease, dispersal and competition. Self-thinning refers to a decrease in population density of a cohort at carrying capacity that results only from intraspecific competition as the individuals within a cohort increase in size and crowd one another. This phenomenon has been extensively studied in plant populations (Weller 1987; Lonsdale 1990). Double logarithmic plots of average plant mass vs. plant density often, but not always, have a slope close to −1.5; i.e., the −3/2 power law of plant self-thinning. As individual plants within a stand increase in size, they shade out their smaller neighbours which eventually die. A self-thinning line occurs in plants because they compete for light, a resource which has several unique properties: it constantly renews, does not accumulate and its input to the population is not affected by the population itself (Begon et al. 1986).

Self-thinning has been investigated infrequently in animal populations. Sessile marine invertebrates compete for space on the substrate in an analagous way to plants, and they also seem to self-thin with a slope of about −1.5 (Hughes and Griffiths 1988). Only Begon et al. (1986) have investigated self-thinning in a mobile animal population, grasshoppers (*Chorthippus brunneus*).

Stream-dwelling salmonid fishes should be ideal subjects for investigating self-thinning. First, when they occur at high densities, they often exhibit density-dependent growth, mortality or emigration (for a review, see Grant and Kramer 1990). Second, they feed primarily on drifting aquatic invertebrates, a resource that shares many characteristics with light: drift constantly renews, does not accumulate and its production may be independent of the density of drift-feeding fishes (Allan 1982). Third, juvenile salmonids often defend feeding territories that increase with body size (Grant et al. 1989; Elliott 1990; Grant and Kramer 1990), providing a potential mechanism for space limitation and self-thinning. A salmonid territory may be analagous to the crown of a tree; both capture energy, increase in size as the individual grows and crowd or shade out neighbours.

If there is a general self-thinning line for mobile animals, there are two possible candidates (Begon et al. 1986). A slope of −1.0 is expected if there is a constant carrying capacity during self-thinning; i.e. the environment can support a fixed biomass regardless of the size of individuals in the cohort. Because metabolic rate is proportional to body mass$^{0.75}$, a slope of −1.33 is expected if animal populations follow a constant-metabolic-rate rule (see Begon et al. 1986). This implies a constant rate of energy input to the cohort. In addition, Grant and Kramer (1990) derived a self-thinning line for stream salmonids assuming that territory size limits density. The slope of this self-thinning line is expected to be −1.08 ($\log_{10}$ mass = $-1.08 \log_{10}$ density + 3.21) because territory size (m^2) increases with body length (cm) ($\log_{10}$ territory size = $2.80 \log_{10}$ length −2.97; model II regression, Sokal and Rohlf 1981), because maximum density (m^{-2}) decreases with body length ($\log_{10}$ density = $-2.80 \log_{10}$ length + 2.97), and because body mass (g) increases with body length ($\log_{10}$ mass = 3.03 $\log_{10}$ length − 1.93). This self-thinning line is slightly different from Grant and Kramer's (1990), because I used a model II regression, which is more appropriate than least-squares regression for describing allometric relationships (Pagel and Harvey 1988).

In this paper, I am concerned with the slope of the self-thinning line, whereas Grant and Kramer (1990) were interested in the elevation of the self-thinning line. I use literature data to calculate self-thinning lines for stream-dwelling salmonids and compare the slopes of these lines with those predicted above: −1.00 (constant biomass), −1.08 (territory size) and −1.33 (constant metabolic rate).

Methods

I searched the literature for data sets which followed cohorts of similar-sized individuals through time. To calculate a self-thinning line, at least three estimates of density and mean weight of the individuals are required. I only included data from riffle and raceway habitats because the fish are highly territorial in these habitats (e.g., Grant and Noakes 1988) and because a territory size regression predicted the maximum density in these habitats quite well (Grant and Kramer 1990).

I used model II regression to estimate the regression equations because it is more appropriate than least-squares regression for estimating allometric relationships (Pagel and Harvey 1988). The confidence intervals for the slopes were calculated using the SE from the least-squares regressions as recommended by Sokal and Rohlf (1981). However, least-squares regressions are shown in the figures for ease of graphical presentation. I used four data sets in the study.

Mason and Chapman (1965) stocked 300 coho salmon (*Oncorhynchus kisutch*) alevins into a stream channel from which individuals could freely emigrate, and monitored the number and size of fish for four months. I used their data for the three riffle habitats of the left channel. Initial densities appeared to be below carrying capacity, as estimated by percent habitat saturation (see Grant and Kramer 1990), so I used only the data for the last four sampling dates to calculate slopes.

Rimmer (1985) stocked rainbow trout (*Oncorhynchus mykiss*) embryos into three stream channels from which fish could emigrate and monitored their size and density for 6 months. Data for the control channel were not included because the densities were well below carrying capacity.

Elliott (1984b, 1985a, 1985b) has monitored the density and growth of brown trout (*Salmo trutta*) in Black Brows Beck from emergence through their second year of life for each year-class from 1967 to 1982. I included three data points from each year-class to calculate a slope: 0+ in May/June, 0+ in Aug./Sept. and 1+ in May/June. I did not include the estimate for 0+ in April because this initial density was often above carrying capacity and as a result there was intense density-dependent mortality in the first month of life (Elliott 1984a).

Allen (1969) compiled literature data on the density and size of stream-dwelling salmonids. These data represent higher than average densities because Allen rejected studies that were so low as to suggest that factors other than space alone were limiting. Allen's data do not represent self-thinning within populations. Nevertheless, if these data represent maximum densities for salmonids in general, then a self-thinning line can be calculated from the between-population data. Clearly such data will be less accurate than within-population data, but were included because of the paucity of within-population data.

Results

In all three riffles of Mason and Chapman's (1965) stream channel, population density declined significantly as mean weight of coho salmon increased (Fig. 1). The model II regression slopes, −1.25, −1.34 and −1.32 for riffles 1, 2 and 3 respectively, did not differ significantly from one another ($P=0.89$, ANCOVA). Mason and Chapman's data were consistent with the constant-metabolic-rate line, but were not consistent with either the constant-biomass or the territory-size thinning lines (Table 1).

Self-thinning appeared to occur in both of Rimmer's (1985) channels since density decreased significantly as mean weight increased (Fig. 2). The slopes of the self-thinning lines did not differ significantly between the two channels ($P=0.39$, ANCOVA).

TABLE 1. Slopes of self-thinning lines calculated from four studies in comparison with three hypothetical lines: constant-biomass (-1.00), territory-size (-1.08) and constant-metabolic-rate (-1.33) thinning lines

		Significantly Different From		
Source	Slope (95 % C.I.)	−1.00	−1.08	−1.33
Mason and Chapman (1965)	−1.30 (−1.42, −1.19)	Yes[a]	Yes	No
Rimmer (1985)	−1.39 (−1.69, −1.10)	Yes	Yes	No
	−1.61 (−2.08, −1.14)	Yes	Yes	No
Elliott (1984b, 1985a, 1985b)	−1.38 (−1.58, −1.21)	Yes	Yes	No
Allen (1969)	−0.96 (−1.16, −0.75)	No	No	Yes

[a] Yes = the 95 % C.I. does not include the hypothetical slope; No = the 95 % C.I. includes the hypothetical slope

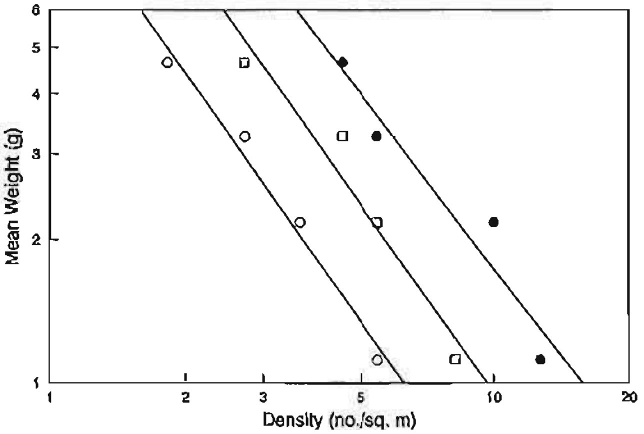

FIG. 1. Self-thinning lines for coho salmon in riffle 1 (solid circles; $Y=30.6-X^{-1.25}$, $r^2=0.93$, $P=0.038$), riffle 2 (open squares, $Y=20.4-X^{-1.34}$, $r^2=0.94$, $P=0.029$) and riffle 3 (open circles, $Y=11.2-X^{-1.32}$, $r^2=0.98$, $P=0.011$) of the left stream channel of Mason and Chapman (1965).

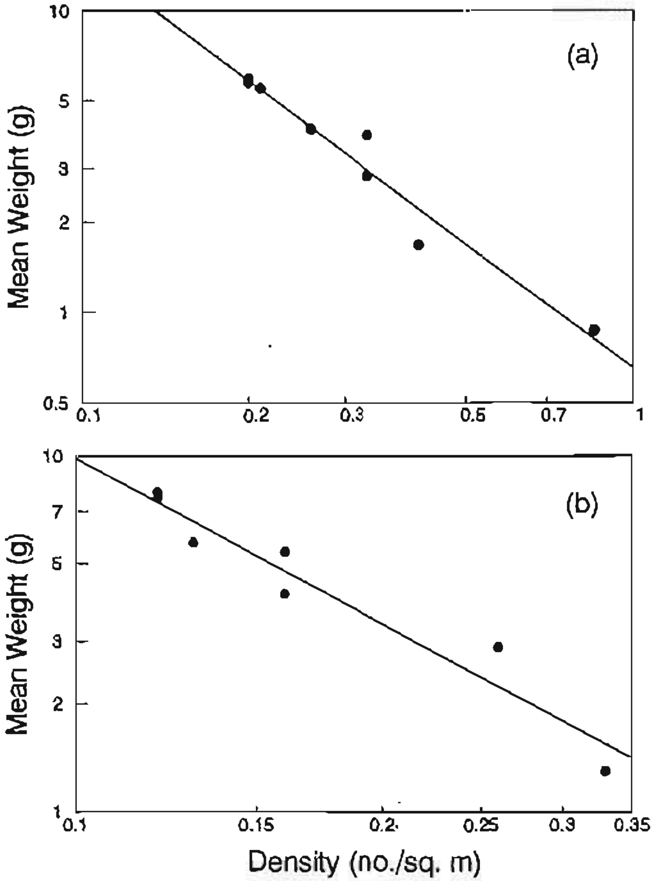

FIG. 2. Self-thinning lines for rainbow trout calculated from Rimmer's (1985) data for (a) the low flow channel ($Y=1.58-X^{-1.39}$, $r^2=0.95$, $P<0.0001$) and (b) the intermediate flow channel ($Y=0.25-X^{-1.61}$, $r^2=0.94$, $P=0.0004$).

Rimmer's data were consistent with the constant-metabolic-rate line, but were not consistent with either the constant-biomass or the territory-size thinning lines (Table 1).

In the combined 16-year data set of Elliott (1984b, 1985a, 1985b), density decreased significantly as mean weight increased in Black Brows Beck (Fig. 3; $P < 0.0001$, ANCOVA). Self-thinning slopes for individual year-classes ranged from −2.32 to −0.95 but did not differ significantly among years ($P=0.59$, ANCOVA). Elliott's data were also consistent with the constant-metabolic-rate line, but not with the constant-biomass or the territory-size thinning lines (Table 1).

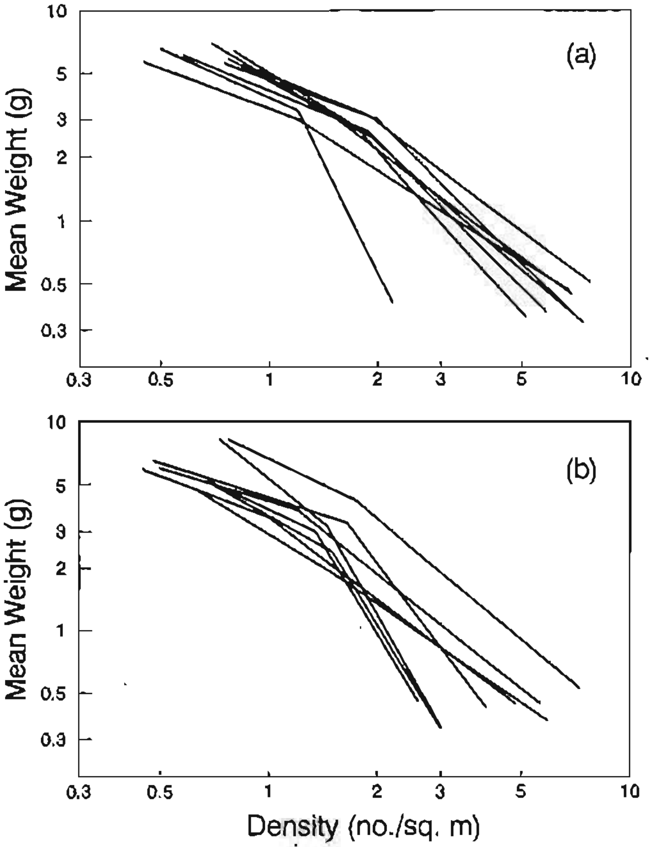

FIG. 3. Self-thinning data for 0+ brown trout in Black Brows Beck (Elliott 1984b, 1985a, 1985b) in year-classes (a) 1967–74 and (b) 1975–82.

In Allen's (1969) data set, density decreased significantly as mean weight increased (Fig. 4; $r=-0.90$, $P<0.0001$). In contrast to the three other studies, Allen's data were consistent with the constant-biomass and territory-size thinning lines, but not with the constant-metabolic-rate line (Table 1).

Discussion

Three of four studies were consistent with the constant-metabolic-rate self-thinning line (slope= −1.33) and did not support either the constant-biomass or the territory-size thinning lines. Allen's (1969) study was the exception, but as I noted above his data may be the least reliable of the four for this sort of analysis. My study, therefore, provides some preliminary support for a self-thinning line with a slope of −1.33 for stream-dwelling salmonids. In the only other study of self-thinning in mobile animals, Begon et al. (1986) suggested that grasshoppers also self-thin with a slope of −1.33.

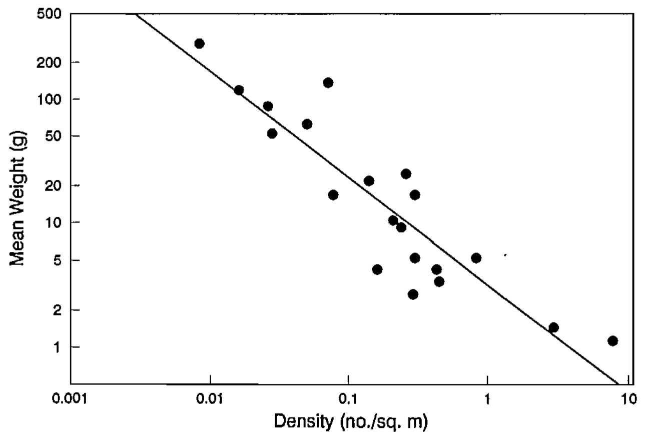

FIG. 4. Biomass vs. length data for stream-dwelling salmonids from Allen (1969). Self-thinning line is $Y=2.72-X^{-0.96}$, $r^2=0.82$, $P<0.0001$).

Grant and Kramer (1990) showed that the inverse of a territory size vs. body size line predicted the maximum density of stream-dwelling salmonids quite well, but did not explicitly consider the slope of the self-thinning line. It is curious that territory size predicts the elevation but not the slope of a self-thinning line for stream-dwelling salmonids. Elliott's long-term study of brown trout may provide an answer to this apparent contradiction. Elliott (1990) has documented a critical period which begins when fry emerge in the spring and lasts between 33 and 70 days. Survival rates are strongly density-dependent during the critical period but proportionate survival occurs after.Survival through the critical period was directly linked to the possession of a territory. If territory size limits population density only during a critical period in the ontogeny of a cohort, then this might explain why territory size predicts the elevation but not the slope of an apparent self-thinning line. Once through this critical period, the cohort would be 'free' to self-thin according to the constant-metabolic-rate line. Thus, the territory-size line predicts the density of salmonids of a given size but the constant-metabolic-rate line predicts the slope of that cohort's trajectory as it self-thins.

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Preference of Juvenile Atlantic Salmon (*Salmo salar*) and Brook Trout (*Salvelinus fontinalis*) for Two Types of Habitat Improvement Structures

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A long-term research program has been developed to evaluate transferability of habitat improvement technology, developed throughout North America, for use with freshwater fish species and endemic conditions in Newfoundland. The initial experiment in this study program in 1990 was to test preferences of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) for two types of habitat improvement structures installed in a controlled flow spawning channel. Six similar sections (replicates), each with three treatment selection options, were constructed in the channel. The arrangement of treatments covered the array of statistical possibilities. Each replicate contained a control option (no habitat modification), a mid-channel option (addition of low-head barrier and boulder cluster) and a stream bank option (addition of artificial undercut banks and wing deflectors). Nine, 5-day-duration experiments were conducted, varying species composition (brook trout only, Atlantic salmon only, and trout and salmon together) and density (low, average, and high densities). Data analysis revealed no difference in preferences between species for the test structures based on volitional residence after 5 days. Both species demonstrated a similar order in preference for the mid-channel, stream bank, and control treatments, respectively. This order of selection was constant at high and low density and low and average density but not high and averge density

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Nous avons mis sur pied un programme de recherche à long terme pour évaluer la transférabilité d'une technologie d'amélioration de l'habitat, mise au point dans l'ensemble de l'Amérique du Nord, qui serait utilisée sur des espèces dulcicoles et dans des conditions endémiques à Terre-Neuve. L'expérience initiale de ce programme d'étude, en 1990, a porté sur les préférences manifestées par des juvéniles de saumon atlantique (*Salmo salar*) et d'omble de fontaine (*Salvelinus fontinalis*) pour deux types de structures d'aménagement installées dans un chenal de ponte à débit contrôlé. On a aménagé dans le chenal six sections similaires comportant chacune trois unités. L'aménagement des unités couvrait le gamme des possibilités statistiques. Chaque section comportait une unité témoin (aucune modification de l'habitat), une unité avec aménagement du centre du chenal (ajout d'une petite levée et d'un enrochement) et une unité avec aménagement des berges (installation de sous-berges artificielles et de déflecteurs). Neuf expériences d'une durée de 5 jours ont été réalisées, avec variation de la composition spécifique (omble de fontaine seulement, saumon atlantique seulement, et omble et saumon ensemble) et la densité (densité faible, moyenne et forte). L'analyse des données n'a révélé aucune différence entre les espèces en ce qui concerne leurs préférences pour les structures du test en fonction de la résidence volontaire après 5 jours. Les deux espèces ont présenté un ordre similaire de préférence pour l'unité d'aménagement du centre du chenal, celle des berges et l'unité témoin. Cet ordre de choix était constant à densité forte et faible et à densité faible et moyenne, mais non à densité forte et moyenne.

Introduction

Atlantic salmon (*Salmo salar* L.) and brook trout (*Salvelinus fontinalis* Mitchill) are the two most abundant and widely distributed freshwater fish in insular Newfoundland (Scott and Crossman 1964). In both the anadromous and resident forms, they are highly valued sports fish in Newfoundland and Labrador and economic benefits are derived from both the recreational fishery (Tuomi 1987) and, in the case of Atlantic salmon, the commercial fishery. In 1985, an estimated $76 million and 2.4 million rod-days were spent angling by 165 000 resident and 4 000 non-resident anglers with a catch of 4.8 million kg, comprised mostly of brook trout (50.8% by number, 6 million fish) and Atlantic salmon (1.4% by number) (DFO and Nfld. Dept. Culture, Recreation and Youth 1988). The participation of Newfoundland residents (27.5%) was the highest of all Canadian provinces (DFO 1987). Atlantic salmon, however, contribute even more significantly to the local economy with direct expenditures by salmon anglers of $13 million in 1985, while the commercial fishery averaged 1021 tons for a value of $4.25 million annually over the period 1984–1989 (DFO 1989).

There is growing interest within Newfoundland and Labrador in salmonid habitat improvement to increase or restore productive capacity of natural and degraded habitats and to provide recreational fishing opportunities. The Department of Fisheries and Oceans' Policy for the Management of Fish Habitat has placed considerable emphasis on habitat conservation, restoration, and development as primary goals towards implementation and delivery of this mandate and in achieving the policy objective of a 'net gain' in habitat.

Fish habitat improvement has been ongoing in other parts of North America for three decades (Duff and Wydoski 1982; Hunt 1988) and, in these regions, there is a wealth of experience and knowledge to assist in design and implementation of habitat improvement initiatives. In Newfoundland and Labrador, however, the concept of improving fish habitat by developing and creating microhabitat conditions preferred by resident salmonids is relatively new, owing largely to lack of large scale urban and other development such as have degraded habitat in other parts of North America. Habitat improvement initiatives in Newfoundland and Labrador have necessarily relied on design and implementation criteria developed in other regions. There is considerable uncertainty as to the applicability of methods, developed elsewhere, for use in Newfoundland with endemic fish species, and the appropriate situations (opportunities) for the implementation of these methods. Additionally, many of the approaches to habitat improvement have been developed for trout species (White and Brynildson 1967; Hunt 1976) and Pacific salmonids (Adams and Whyte 1990). There is limited experience to assess the value of such techniques to benefit juvenile Atlantic salmon.

To address these concerns and knowledge gaps, a long-term, multi-study research program has been developed by the Department of Fisheries and Oceans to assess interspecific preferences of juvenile Atlantic salmon and brook trout in Newfoundland and Labrador for various improvement structures and the habitat attributes they create. This paper presents the initial results from this research agenda.

Materials and Methods

An abandoned control flow spawning channel at the Noel Paul's Brook incubation facility on the Exploits River watershed was modified in 1990 to create similar physical conditions in a contiguous study zone. The channel was brought to uniform gradient (0.41 % slope), substrate (gravels 2.5–7.5 cm diameter) and width (3 m). The margins of the channel were stabilized with large rip-rap (boulders 15.0–60.0 cm diameter). The channel was then divided into 6 replicates of 20 × 3 m. Each replicate consisted of a control, mid-channel and stream bank treatment type, each 6.67 m in length. The control reach received no further modification. The mid-channel reach was altered to contain a low-head barrier (with 2 notches and associated plunge pools) and a boulder cluster consisting of 5 large boulders (30–60 cm diameter) in the centre 1 m of the channel. The stream bank reach was modified to contain 2 structures creating artificial undercut bank (mini-lunkers) and 2 wing deflectors. Replicates were partitioned from each other with portable conduit weir material (Anderson and McDonald 1978) with 1.0 m of 0.5 cm vexar attached to the weirs and extending into the stream bank and substrate to prevent fish movement between replicates. Figure 1 details a representative replicate, the individual treatment types, and the configuration of the habitat improvement structures. Six replicates, containing all possible combinations of the treatment types, were utilized to remove any statistical bias. For the purposes of this study, all stream bank vegetation was removed so that natural overhanging cover and shade would not bias the results (these are variables to be evaluated in future research).

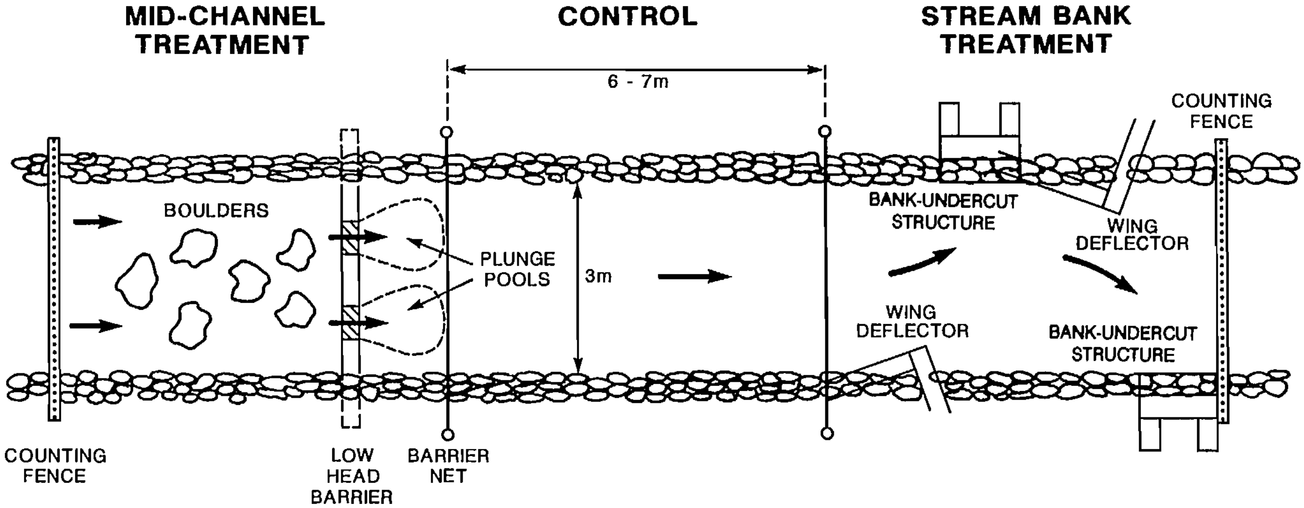

FIG. 1. Schematic representation of an experimental replicate showing stream dimensions and configuration of habitat improvement structures.

TABLE 1. Experiments conducted as part of the study of species preference for habitat improvement structures.

Experiment	Dates	Species mix[a]	Density level[b]	No. fish per 100 m^2
1	26/07/90 to 30/07/90	BT	L	16
2	26/08/90 to 30/08/90	BT	M	23
3	22/08/90 to 26/08/90	BT	H	34
4	30/07/90 to 03/08/90	AS	L	16
5	03/07/90 to 07/07/90	AS	M	23
6	12/07/90 to 16/07/90	AS	H	34
7	06/08/90 to 10/08/90	BT/AS	L	16
8	08/07/90 to 12/07/90	BT/AS	M	24
9	22/07/90 to 26/07/90	BT/AS	H	36

[a] BT = Brook trout, AS = Atlantic salmon, BT/AS = Equal mix of both species.

[b] L = Low, M = Medium, H = High.

Nine, 5-day experiments were conducted from July 3 to August 30, 1990 (Table 1). Experiments consisted of evaluating preference for the selected habitat improvement structures (treatments) under conditions of varying species composition (brook trout only, Atlantic salmon only and an equal mix of salmon and trout) and density (low, 16 fish·100 m^{-2}; average, 23–24 fish·100 m^{-2}; and high, 34–35 fish·100·m^{-2}). Preference was defined as selection for volitional residence at the end of each 5-day test. Fish used in the study were collected from neighbouring streams, held at the incubation facility in cages, and fed as required. On day 1 of each experiment, fish were sorted by size and an equivalent sample of the appropriate species mix and density were introduced into each replicate. Fish were allowed to distribute within each replicate for 5 days. On day 5, barrier nets were dropped in place between the treatment types and fish were removed by electrofishing. For each experiment, fish were identified as to replicate, treatment, and species; weighed (nearest g), measured (fork length to nearest mm), a representative subsample of scales collected for subsequent aging, and data entered on to coding sheets. At the completion of each experiment fish were released back into natural streams; i.e., new fish were used for each experiment. Fish used in the study were immature juveniles ranging from yearlings to 3-year-old fish. Brook trout ranged from 46 to 207 mm in length (mean of 109.8) and 1.1–91.4 g in weight (mean of 18.6) while Atlantic salmon ranged from 39 to 298 mm in length (mean of 93.4) and from 1.6 to 61.0 g in weight (mean of 11.3).

Flows (mid-column velocities) within the treatment types were variable with the control, stream bank and mid-channel having an average current velocity (range) of 12.15 m·s^{-1} (10.0–15.0), 17.17 m·s^{-1} (11.2–29.0) and 9.32 m·s^{-1} (7.9–10.8), respectively. Velocity was measured at 1.0 m intervals in the centre of each treatment type with an Ott Current Meter (model C2, propeller type). Depths, obtained from 3 m measurements equidistant across the width at every metre of length, were consistent, with average depths for the control, stream bank, and mid-channel of 31.6, 29.1, and 32.3 cm, respectively.

Results

The underlying contingency table of habitat by species mix by density was fitted to a linear model as in Grizzle et al. (1969) for analysis. The response category, habitat selection, can be considered ordinal with respect to cover and a set of scores was chosen to represent the amount of cover in each treatment type; 0 for the control, 0.5 for the mid-channel and 1.0 for the stream bank. This was used to analyze the mean score. The independent variables, species mixture and density, each had 3 levels (i.e., trout only, salmon only and trout and salmon mix for species mixture and low, average and high density for density level), respectively. In this analysis, the average density was to approximate the carrying capacity of the area. The data were summed over the replicates for each of the species mix, density levels, and treatment type combinations. The mean score was then fitted to the independent variables using weighted least squares.

Initially a full or 'saturated' model : mean score = density species density*species was fitted. The model uses all the degrees of freedom in the model space. The goal of the analysis was to find the simplest model that describes the data so non-significant effects are moved to the error space sequentially, resulting in the final model: mean score = density. Pairwise contrasts were constructed to find differences in the mean response for the three density levels.

The data were initially analyzed to determine if there existed any differences in species preference for the habitat improvement structures. The results of this analysis revealed no species preference for any of the structures so the species data was combined. The fish tested in this study chose the mid-channel treatment over the stream bank treatment over the control, irrespective of population density (Tables 2 and 3). Similarities existed between high and low and low and average densities but not high and average density (Table 3).

Discussion

Habitat selection by juvenile Atlantic salmon and brook trout is highly dependent on competitive

TABLE 2. Percentage recovery of fish by treatment type examined in this study.

	% Recovered		
Species	Control	Mid-Channel	Stream Bank
Trout	18.0	46.0	36.0
Salmon	17.8	45.7	36.5
Salmon & Trout	16.0	52.0	32.0
All Fish	17.0	48.5	34.5

TABLE 3. Details of model analysis.

Analysis of Source of Variation

Source	df	Chi-Square	Probability
Intercept	1	2560.25	0.0001
Density Level	2	6.37	0.0415
Residual	6	5.52	0.4794

Analysis of Contrasts

Contrast	df	Chi-Square	Probability
Low vs Average Density	1	1.02	0.3137
Low vs High Density	1	1.15	0.2837
Average vs High Density	1	6.33	0.0119

interactions, and habitat preferences are in part, related to whether the species are allopatric or sympatric (Gibson and Cunjak 1988; Gibson 1988). In areas where fish species diversity is low, as in insular Newfoundland, a wider range of habitat types can be occupied (Gibson et al. 1993). This experiment addressed habitat preferences by brook trout and Atlantic salmon in relation to habitat improvement structures/techniques to assist in technology transfer to the Newfoundland and Labrador region, and to guide public sponsored improvement and restoration projects. An understanding of habitat selection by juvenile salmon and trout, under conditions of inter- and intra-specific competition, is important in order to design and implement habitat improvement and restoration projects to meet their intended objectives. Certain projects may have a generic objective of 'increasing fish production', while others may be directed at increasing production of, or providing holding areas for, large trout in order to enhance angling opportunities.

The considerations used to design the habitat improvement devices used in our experiments were based on known response to habitat by juvenile salmon and trout; that salmon tend to occupy faster, flowing waters in the centre of streams and rivers over coarse substrates while trout tend to occupy either the margins of streams and rivers or pools, characterized by slower, deeper water often associated with riparian or instream cover (Gibson et al. 1993; Gibson and Power 1975). Both species tend to occupy a wider range of habitats when inter-specific competition and predation are low (Gibson et al. 1993). Gibson et al. (1987), on the Highland River in western Newfoundland, found juvenile salmon biomass highest in open areas with coarse substrate, while trout biomass was greatest in small streams with stable discharge (headwater streams), lower velocities, deep water, and with overhanging cover. Gibson (1988) also found that trout biomass was positively correlated with instream cover and stable water flows in the Experimental Rivers area, Avalon Peninsula, in eastern Newfoundland.

Our experiment revealed no difference in preference between trout and salmon for the two stream improvement treatments tested: the stream bank (wing deflector and 'mini-lunker') versus the mid-channel (boulder cluster and low-head barrier) structures. Both species preferred the mid-channel structures over the stream bank treatment over the control area (Table 2). Increasing density displaced both species equally into the less preferred treatments, the stream bank and control sections. This may in part be explained by the absence of true pool habitat in association with the stream bank treatment structures. Pool scouring as a result of wing deflectors did not occur because of the regulated (constant) discharge. It is also possible that velocities associated with the structures were unsuitable for either species.

Gibson et al. (1993) and others have indicated that habitat selection and distribution of juvenile salmon and trout is related to a number of factors and attempting to relate habitat preference to any one variable may be meaningless. For example, preference of juvenile salmon for coarse substrate may, in part, be related to velocity shelters behind the substrate, turbulent water surface (as a cover variable) and visual isolation (Gibson 1988). The absence of riparian vegetation in association with the stream bank treatment may have reduced the preference for these structures, particularly by brook trout, whose preference for habitats associated with overhanging cover is well documented (Gibson and Keenleyside 1966; Gibson et al. 1993). Future research will address the influence of velocity and cover on habitat selection and the combination of variables that contribute to observed preferences.

The apparent preference of both species for the mid-stream structures may be primarily related to the velocity spectrum and cover these structures provided. Interestingly, the mid-channel treatment had the lowest mean velocity of the experimental treatments, 9.32 m·s^{-1}, as opposed to 17.17 m·s^{-1} for the stream bank treatment and 12.15 m·s^{-1} for the control. Kalleberg (1958) has observed that velocity plays a large role in determining the aggressiveness and territoriality of juvenile salmon and that schooling tendencies were more evident as velocities diminished approaching zero. He reported that competition for space depends partially upon the tendency for aggressive, territorial behaviour, the density of the population (available space), and the degree of visual isolation. The mid-stream treatment, with five large boulders and plunge pools (and turbulence) associated with a low-head barrier would afford more diversity in habitat in terms of velocity and cover as well as more discrete holding areas with some degree of visual isolation. Selection of holding areas and behaviour are also subject to change with habitat type and season (Gibson et al. 1993). Individuals may be territorial or, in certain circumstances, school according to conditions of velocity, temperature, food, social interactions, and other factors (Gibson 1988).

Our study suggests that the stream bank structures used and/or the microhabitat features created by them, were not preferred by either species, whether in conditions of allopatry or sympatry and regardless of increasing density. It is likely that the appropriate conditions of velocity, depth and, in particular, cover were not created to provide preferred trout habitat features. Stewart (1970) noted that mean depth, underwater overhanging rock cover, undercut banks and areas of deep turbulent water were important variables determining density of brook trout and rainbow trout (*Oncorhynchus mykiss*). 'Lunker' structures, as an undercut bank-creating device, are directed at providing habitat (holding areas) for larger, older trout, in part to enhance recreational fisheries (Hunt 1976, 1988). The technique may not be well suited to smaller trout (i.e., 1+, 2+ and 3+ year old fish), thereby limiting their broader application. Wing deflectors are directed at improving channel sinuosity, creating diversity with respect to pool and riffle sequences, and to induce scouring of deep channels and pools (White and Brynildson 1967). In our experiment, these structures appear not to have created the desired microhabitat features and indeed this treatment had the lowest mean depth (29.1 cm versus 32.3 for the mid-channel and 31.6 cm for the control) and highest velocity (17.17 $m{\cdot}s^{-1}$; as opposed to 9.32 $m{\cdot}s^{-1}$ for the mid-stream treatment and 12.15 $m{\cdot}s^{-1}$ for the control) of the experimental treatments.

There is a wide range in habitat occupied by juvenile salmon, with considerable overlap in habitat preferences of trout. Yearling brook trout are often found in shallow, riffle areas in association with salmon parr, and this overlap in habitat, can negatively affect the growth of yearling trout (Saunders and Smith 1962). Salmon parr generally occupy holding positions closer to the substrate than do trout in faster flowing, riffle areas, often resting in direct contact with the substrate (Gibson 1988). Such niches allow parr to utilize reduced water velocities at the stream bottom thereby expending less energy than would trout suspended above the substrate, affording them a competitive advantage. In their preferred riffle habitat, juvenile salmon parr are also usually territorial during the growing season (Gibson 1988). Conversely, larger salmon parr and trout tend to occupy pool habitats. In pools, parr are generally less aggressive than in riffles, consequently trout gain a competitive interspecific advantage in this deeper, slower type of habitat (Gibson and Dickson 1984).

There are a variety of other considerations that may have influenced the selection of habitat by the experimental fish used in our study. Kalleberg (1958), for example, noted that aggressive behaviour of juvenile salmon was subdued after being exposed to conditions of overcrowding. Thus it is possible that holding fish in cages prior to each of our experiments suppressed the normal expression of aggressiveness and territoriality. Feeding, or rather the inability to feed while in the stream channel, may also have played a role in the social interactions involved in habitat selection. Our experimental channel is isolated from the main channel of Noel Paul Brook and is not subject to normal sources of insect drift. Additionally, the study channel was modified just prior to the initiation of the experiment, and the normal process of allochthonous and autochthonous production of food and colonization of the stream channel by invertebrates, in drift, had not occurred.

Under the experimental conditions of this study, both species preferred mid-channel structures (boulders and low head barrier), regardless of whether each species was tested individually, or sympatrically. Increasing density displaced both species equally into the less preferred habitat treatments; the stream bank structures (wing deflector, undercut bank structure) or the untreated stream reaches (control). The stream bank structures apparently did not create habitat features (depth, velocity, cover) preferred by either species, especially brook trout. The hydrologic control of the study stream eliminated the natural variation in discharge that would have created greater diversity in stream features preferred by juvenile trout. These considerations indicate that the range in discharge of a candidate stream would be an important factor in the selection of the appropriate improvement devices.

Lentic habitats are generally considered atypical habitats for juvenile salmon. However, use of such habitat can be significant where competition and predation are low (Gibson 1973; Chadwick and Green 1985). Atlantic salmon juveniles in insular Newfoundland use a wider range of available habitat in both lentic (Pepper 1976; Pepper et al. 1985) and lotic habitats (deGraff and Bain 1986) than elsewhere. Consequently, initiatives involving habitat improvements or alterations in Newfoundland need to consider species diversity and tailor the projects accordingly. The depauperate fish fauna of Newfoundland will be an important consideration in the transfer of habitat improvement technology for use with endemic species and environmental conditions locally.

Our experiment is the initial study in a long-term research program to address the transfer of stream improvement technology to the Newfoundland region, primarily to support publically sponsored stream improvement and restoration initiatives. Future research will address a number of related issues; eg., effects of size and/or age class, density, competitive interactions (inter- and intra-specific), hydrologic conditions (discharge and velocity), and riparian features. Preference for a variety of other stream improvement devices will also be investigated in the context of microhabitat aspects (eg., focal depth, velocity, substrate cover; proximity to other fish, structures, shade, turbulence, feeding, etc.).

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A 25-Year Study of Production of Juvenile Sea-Trout, *Salmo trutta*, in an English Lake District Stream

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ELLIOTT, J. M. 1993. A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English Lake District stream, p. 109–122. *In* R. J. Gibson and R. E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

The population dynamics of sea-trout, *Salmo trutta*, have been investigated continuously in Black Brows Beck (northwest England) from 1966 to 1990. The chief factors affecting survival, growth and production are identified and their effects summarised in a series of mathematical models. Survivor density and loss-rates at different stages in the life cycle are strongly density-dependent on egg density. 'Key-factor analysis' showed that population density throughout the life cycle is regulated by density-dependent survival in the early life-stages. Mean growth is not density-dependent but is affected chiefly by water temperature, a secondary factor being the size of the newly emerged fry. Mean annual production over 24 years is 23.40 g m^{-2} (range 8.86–33.90 g m^{-2}) and mean production for 22 year-classes is 23.00 g m^{-2} (range 7.59–33.88 g m^{-2}). Most production variation (74.2%) between year-classes is due to the combined effect of density-dependent survival (56.7%) and density-independent growth (17.5%). Such long-term investigations are essential for the development of realistic models to predict the optimum fish density and the maximum attainable growth and production in different habitats.

La dynamique de la population de truite de mer (*Salmo trutta*) a été étudiée en continu de 1966 à 1990 à Black Brows Beck (nord-ouest de l'Angleterre). Nous avons repéré les principaux facteurs touchant la survie, la croissance et la production, et leurs effets sont résumés en une série de modèles mathématiques. La densité des survivants et les taux de perte à différents stades du cycle biologique présentent une forte dépendance par rapport à la densité des œufs. L'analyse des facteurs clés a montré que la densité de population sur l'ensemble du cycle biologique est régulée par la survie dépendante de la densité dans les premiers stades biologiques. La croissance moyenne n'est pas dépendante de la densité, mais elle est affectée principalement par la température de l'eau, avec pour facteur secondaire la taille de l'alevin émergeant. La production annuelle moyenne sur 24 ans est de 23,40 g m^{-2} (fourchette de 8,86–33,90 g m^{-2}), et la production moyenne pour 22 classes annuelles est de 23,00 g m^{-2} (fourchette de 7,59–33,88 g m^{-2}). La plus grande partie de la variation dans la production entre les classes annuelles (74,2 %) est due à l'effet combiné de la survie dépendante de la densité (56,7 %) et de la croissance indépendante de la densité (17,5 %). De tels travaux à long terme sont essentiels à l'établissement de modèles réalistes permettant de prédire la densité optimale de poissons et la croissance et la production maximales qui peuvent être atteintes dans des habitats différents.

Introduction

The production rate of a fish population is defined as the total elaboration of fish tissue during a known time interval, including that formed by fish that do not survive to the end of the time interval (Ivlev 1966; Chapman 1978a,b). As production is the product of growth and temporal change in population density, it provides an excellent measure of the quantitative performance of a fish population in any particular environment (Le Cren 1972). Many studies have been made on salmonid populations in streams (see reviews by Le Cren 1972; Waters 1977, 1988, Chapman 1978a,b; Mann and Penczak 1986; Gibson 1988).

Mann and Penczak (1986) summarized production values for eight species of salmonids, with 32 publications providing 85 estimates. The most frequent were for *Salmo trutta* L. (38 values, range 0.14–54.70 g · m^{-2} · yr^{-1}) and *S. salar* L. (16 values, range 0.22–11.10 g · m^{-2} yr^{-1}). These suggested a maximum value of c. 30 g · m^{-2} · yr^{-1}. Later work generally confirms this conclusion, apart from a few higher estimates (see review by Waters 1988). The chief weakness of these estimates is that they are based on data collected over relatively short periods of time, usually less than 5 years, and therefore provide little information on natural variation in production rates. Such information is essential before meaningful comparisons can be made between streams.

The present investigation is part of a long-term study of the population dynamics of migratory trout, *Salmo trutta*, in Black Brows Beck in the English Lake District. Further results can be found in seventeen publications (Elliott 1984a,b; 1985a,b,c,d; 1986; 1987a,b; 1988, 1989a,b,c,d,e; 1990a,b). The overall objective is to provide mathematical models describing the complex mechanisms regulating the numbers, growth and production of brown trout, including sea-trout, because such work is essential for the conservation and management of fish stocks.

A previous review summarised the results of this investigation for the years 1966–83 (Elliott 1985d). The present contribution includes additional information from 1984–90, a period in which some marked fluctuations occurred, and also emphasises production for the first time.

Materials and Methods

Study Area and Field Sampling Methods

Black Brows Beck, a small stream in northwest England, serves as a nursery for the progeny of sea-trout. Such nursery streams are economically important because sea-trout fisheries are a valuable resource with a minimum value of £55 million in England and Wales (Elliott 1989b). The stream is a typical lowland tributary (altitude c. 70 m 0.D.) of the drainage system of the River Leven and is only about 8 km from the upper tidal limit of the river so that migrating smolts can soon reach the estuary and returning adults can reach the spawning grounds in less than a day. The conductivity of the stream is low at about 100 µS cm^{-1} (k_{25}) with a calcium concentration of about 0.4 m eq l^{-1} and a pH range of 6.7–6.9. Water temperature ranges annually from 0.1 to 18°C with a mean of about 9°C.

Spawning occurs in November and December, eggs usually hatch in February/early March and the alevin stage ends in late April/early May when the fry disperse from the redd. The parr stage lasts about 2 years and most trout start to migrate downstream to the estuary at the start of their third year (age 2+ years). In a few years, a smaller number of fish do not migrate until one year later. Some mature males in their third year return from the sea/estuary in the year of their smolt migration after spending only one summer away from fresh water. Most spawners are males and females in their fourth year (age 2/1+ years, i.e. 2 years in fresh water, over 1 year in sea/estuary). A very small number of females in their fifth year spend two winters at sea and some of these fish have been caught as they spawned for a second time.

Electrofishing is used to catch trout from known areas of stream throughout the year. Samples are always taken (1967–90) at the end of May or early June and at the end of August or early September. The study section of 60 m^2 is divided by block nets into six subsections, each with a surface area of 10 m^2. Additional samples have been taken at more frequent intervals in some years. All fish in the study section are removed, counted and returned live unless a small sample is required for gut analyses. Each fish is measured (fork length) and used to be weighed, but this is now rarely done because length-weight relationships are well established.

Since November 1966, an annual census has been made of redd number and hence the number of spawning females (there is never more than one female per redd). Excavations of redds elsewhere in the stream provided information on the number of eggs per redd for early, middle and late spawners (Elliott 1984a). It was thus possible to estimate egg density from the number of redds and the time of spawning. Each year-class is named after the year in which eggs hatched, not the year in which they were laid. Occasional samples are taken of adults returning to spawn and scales are removed for ageing. Direct observations are made of spawning behaviour and the territorial behaviour of the juveniles.

More details of the study area and sampling methods can be found in the seventeen publications mentioned in the introduction.

Synopsis of Equations and Models

A large amount of time is spent on data analysis and large-frame computer facilities are required for fitting the more complex curvilinear models.

The six, most-frequently used, density-dependent models were tested on the population-density data (Elliott 1985b). The following two-parameter model provided significant fits for all life-stages:

$$(1) \qquad R = aS\exp(-bS)$$

where R = number of survivors at different stages in the life cycle, S = number of eggs at the start of each year-class, a and b are parameters estimated by non-linear least squares, using a pseudo-Gauss–Newton algorithm. This model is sometimes called the stock-recruitment curve of Ricker (1954) but it is a common density-dependent model that has been used in many terrestrial studies (see references in Elliott 1985b).

Equation (1) indicates a linear relationship between loss-rate (ln (S/R)) and egg density (S):

$$(2) \qquad \ln(S/R) = c + bS$$

where c and b are parameters estimated by linear regression (the term 'loss-rate' is used instead of mortality rate because a density decrease could be due to mortality or migration or both).

The fit of each model is assessed by F-values for the variance ratios and the proportion of the variance of R, or ln (S/R), explained by variations in S is estimated by the coefficient of determination (r^2):

$$(3) \qquad r^2 = 1 - [(1 - r_s^2)(n - 1)/(n - k)]$$

where n = number of pairs of R and S, k = number of parameters, r_s^2 = (sum of squares due to regression)/(total sum of squares about the mean values of R or ln (S/R)). The null hypothesis is that R, or ln (S/R), is not dependent on S.

Loss-rates between life-stages are compared by 'key-factor analysis' in which population density is expressed on a logarithmic scale so that the total loss-rate is the sum of loss-rates between successive life-stages. Actual values for total loss-rates (K) between the egg stage (S) and 3+ female spawners (R_5) are calculated directly from the data, assuming a sex ratio close to one ($K = \ln(0.5S/R_5)$), and estimated values of K are calculated from a simple model for loss-rates between all intermediate life-stages (k_0 to k_5, see Fig. 3, 4):

$$(4a) \quad K = k_0 + k_1 + k_2 + k_3 + k_4 + k_5$$

As $k_0 \approx 0$, k_3, k_4, k_5 are fairly constant over most year-classes, k_2 is negatively related to k_1, and k_1 is positively related to S, then this equation reduces to:

$$(4b) \quad K = a + bS$$

where a and b are parameters estimated indirectly from summation of the constant k-values and the linear regressions between k_2 and k_1, and between k_1 and S (see also Elliott 1985a,d; 1987a).

A growth model developed from laboratory experiments (Elliott 1975a,b) estimates changes in the mean wet weight of trout throughout each year-class on successive sampling dates:

$$(5) \quad W_n = [b_1 (a + b_2 T) t_n + W_\circ^{b_1}]^{1/b_1}$$

where W_n = mean wet weight (g) after t_n days at T °C, $W_\circ$ = mean wet weight of newly emerged fry at $t_\circ$ days, and values of the constants a, b_1 and b_2 are given in Elliott (1975a).

Increases in wet weight are estimated at intervals of two weeks, using mean water temperatures and estimates of $W_\circ$ for each year-class. Fish samples in the first winter of the life cycle have shown that growth ceases for about 6 months (Elliott 1985c). It is therefore assumed that growth ceases from 15 September to 15 March, even though water temperatures are sometimes theoretically high enough for some growth to occur. There is no similar cessation of growth in the second winter of the life cycle.

Production (Pg m^{-2}) and mean biomass ($\bar{B}$g m^{-2}) are estimated by standard equations (Chapman 1978b):

$$(6) \quad P = \Delta t \, G \, \bar{B}$$

where G = mean specific growth rate in wet weight per day, t = time interval in days over which P,G and $\bar{B}$ are measured. Mean biomass ($\bar{B}$) is estimated from initial biomass at the start of Δt and the difference between specific rates of mortality (Z) and growth (G), using equations from Chapman (1978b) for $G>Z$ and $G<Z$.

The relationship between total production for a year-class (Pg m^{-2}) and initial egg density (S eggs m^{-2}) is described by equation (1) with P substituted for R. This equation is the basis of a new model incorporating mean live weight (Wg) of third year trout on 30 April. The latter weight was estimated by equation (5) and provides a measure of total growth during the freshwater phase of the life cycle (Elliott 1985c):

$$(7) \quad P = aS \exp(-bS) - c + dW$$

where a,b,c,d are parameters estimated by the same methods used to fit equation (1).

Results

Population Density and Survival

Survival was density-dependent; the number of survivors at different stages in the life cycle was related to the number of eggs at the start of each year-class (Fig. 1a). The density-dependent relationship was well described by equation (1) which was a significant fit to all five life-stages (Table 1). Coefficients of determination (r^2) indicated that variation in initial egg density between year-classes could explain 96% of the variation in survivor density of 0+ fish in May/June but subsequent values were lower; 70% for 0+ fish in August/September, only 21% for 1+ fish in May/June, 50% for 1+ fish in August/September, and 58% for spawning females in November/December. Loss-rates

TABLE 1. Stock-recruitment relationships for different life-stages of migratory trout in Black Brows Beck: estimates of the parameters a and b in equation (1) and c and b in equation (2) (parameters estimated by non-linear least squares and linear regression, respectively) and coefficients of determination (r^2 in equation 3) with significance levels for F-values (*$P<0.05$, **$P<0.01$, ***$P<0.001$).

Stage	Year-class (n)	a (SE)	b (SE)	r^2	c (SE)	b (SE)	r^2
R_1: 0+ parr (May/June)	24	0.488 (0.0122)	0.000415 (0.000007)	0.96***	0.717 (0.0263)	0.000412 (0.00000581	0.97***
R_2: 0+ parr (Aug/Sept) exc. 83,84,80	21	0.0872 (0.00515)	0.000277 (0.000013)	0.70***	2.366 (0.0579)	0.000290 (0.0000124)	0.97***
R_3: 1+ parr (May/June) exc. 83,84	21	0.0336 (0.00332)	0.000266 (0.000021)	0.21*	3.295 (0.0979)	0.000281 (0.0000211)	0.90***
R_4: 1+ parr (Aug/Sept) exc. 68,83,84	20	0.0369 (0.00405)	0.000328 (0.000026)	0.50***	3.265 (0.117)	0.000339 (0.0000247)	0.91***
R_5: 3+ females (Nov/Dec) exc. 76,83	19	0.00545 (0.000797)	0.000359 (0.000039)	0.58***	5.055 (0.238)	0.000442 (0.0000513)	0.81***
Total eggs produced exc. 83	20	5.467 (0.981)	0.000359 (0.000047)	0.44**	-1.771 (0.225)	0.000415 (0.0000488)	0.80***

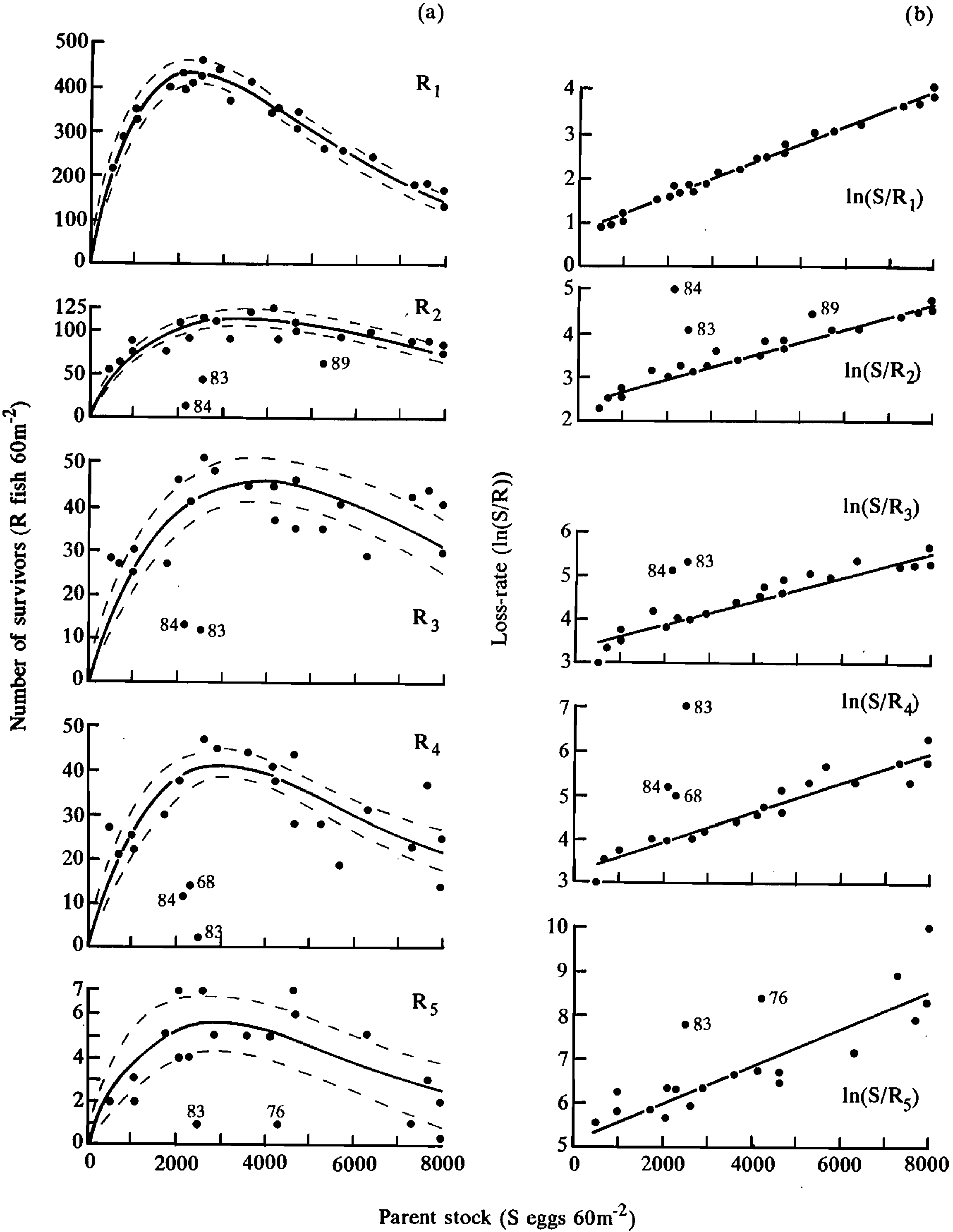

FIG. 1. Relationship between: (a) number of survivors (R fish per 60 m^2) at different stages in the life cycle (R_1 - R_5) and the parent stock (S eggs per 60 m^2); curves were estimated from equation (1) and the broken lines indicate 95% C.L. for each curve (year-classes are given for some values of R_2, R_3, R_4 and R_5 when these values were excluded from the data set used to fit the curve); (b) loss-rates (ln (S/R)) and the parent stock (S); linear regression lines were estimated from equation (2) (year-classes given for values excluded from the regression analysis). [Life stages: R_1, 0+ parr in May/early June; R_2, 0+ parr August/early September; R_3, 1+ parr in May/early June; R_4, 1+ parr in August/early September; R_5, 3+ females spawning in November/December}.

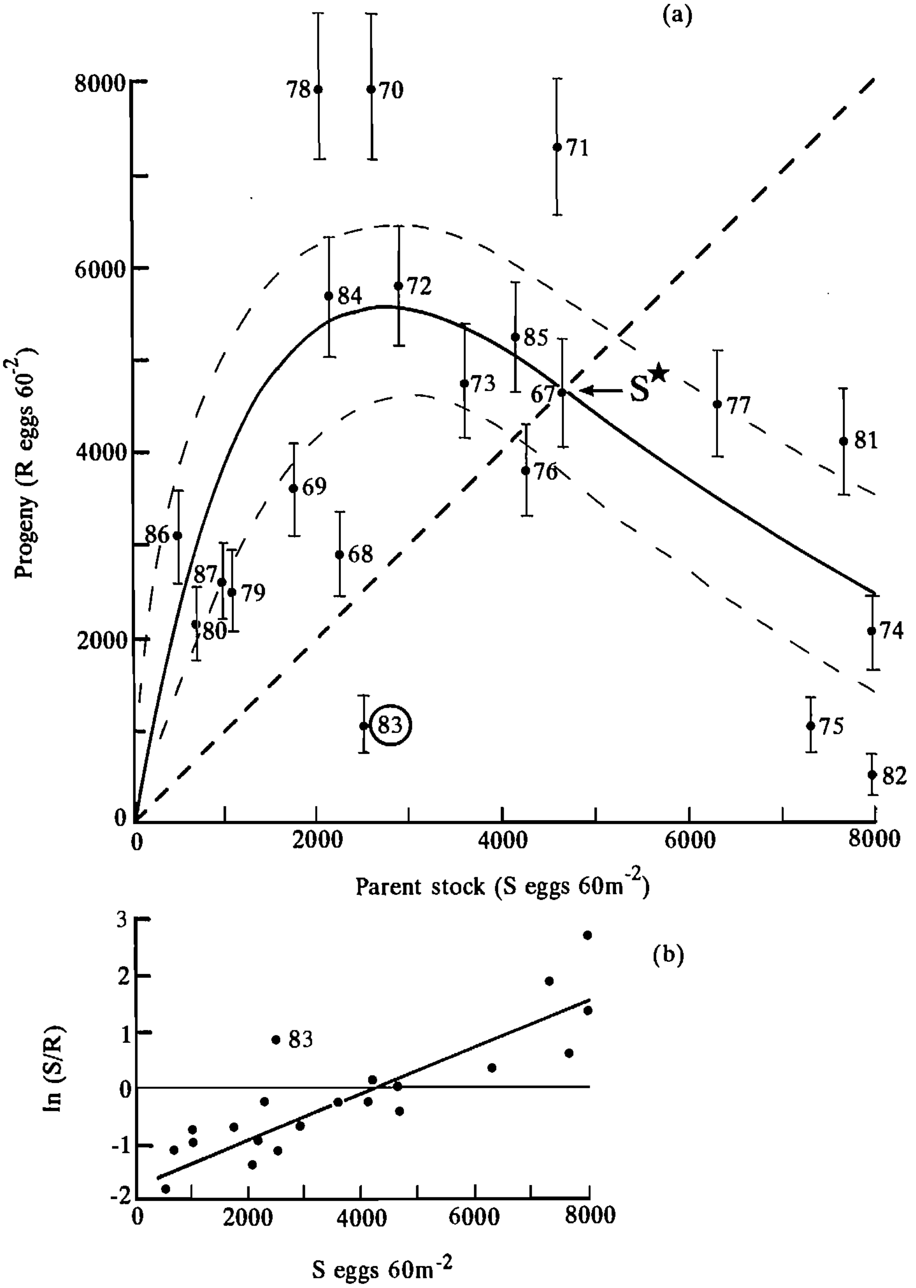

FIG. 2. Relationship between: (a) total eggs produced by each year-class (R eggs per 60 m^2) and the parent stock at the start of the year-class (S eggs per 60 m^2); stock-recruitment curve was estimated from equation (1), broken lines indicate 95% C.L. for each curve and year-class is given for each point which is the mean ±2 SE (value for 1983 was excluded from the analysis); equilibrium density (S^* eggs per 60 m^2) = 4731 eggs (equivalent to 79 eggs m^{-2}); (b) loss-rate (ln (S/R)) and the parent stock (S); linear regression line was estimated from equation (2) (value for 1983 was excluded from the analysis).

in the different year-classes were strongly density-dependent on egg density with all r^2 values >0.80 (Fig. 1b, Table 1).

Significant departures from the model were chiefly for year-classes affected by the summer droughts of 1969, 1976, 1983, 1984, 1989 (points labelled in Fig. 1). In each of these years, there was a period of at least 3–4 weeks without rain in June, July or August, and parts of the stream bed were left dry. The droughts usually affected only one life-stage and long-term effects on the population density of spawning females were evident for only the 1976 and 1983 year-classes (R_5 values Fig. 1). As is shown later, growth was poor in these year-classes (Fig. 5) and the small size of the smolts with subsequent high mortality at sea could be one reason for the low numbers of returning females.

The relationship between total egg production by the surviving progeny and egg density at the start of a year-class was also density-dependent (Fig. 2a); the equilibrium point (S^* on Fig. 2a) was equivalent to 79 eggs m^{-2} and the slope at this point indicated that population density was essentially stable. Each point is the egg density at the beginning and end of a four-year period and yet the fit of equation (1) was very good ($P<0.01$) with an r^2 value indicating that 44% of variation in egg production could be explained by variation in initial egg density. This relationship was emphasised by the strong relationship between total loss-rate over the 4-yr period and initial egg density (Fig. 2b, Table 1); the latter accounting for about 80% of the variation in the former. Only the 1983 year-class clearly departed from these relationships, and this was the only year-class out of twenty-one to be affected in the long-term by a summer drought.

'Key-factor analysis' was used to discover if the density-dependent effect throughout the life cycle was due to its strong influence in the early stages or to a continual density-dependent effect between different life-stages. The total loss-rate (K) between the egg stage and female spawners was partitioned into six loss-rates (k_0-k_5 in equation 4a). A graphical comparison (Fig. 3) showed that loss-rates were close to zero between the egg and alevin stages (k_0), fairly constant (excluding year-classes affected by summer droughts) for the first summer (k_2), first winter (k_3), second summer (k_4) and second winter plus post-migration period in the sea/estuary (k_5). The loss-rate in the first spring of the life cycle (k_1) provided the highest contribution to K in most year-classes.

There were clear positive relationships between k_1 and initial egg density (S eggs per 60 m^2) and between k_2 and 0+ parr density in late May/early June (R_1), but no significant relationships were obtained for k_3, k_4, k_5 (Fig. 4). The three latter values were fairly constant when high values associated with droughts were excluded (named year-classes in Fig. 4). It was found that k_2 was inversely related to k_1 ($k_2 = 1.858–0.285\ k_1$).

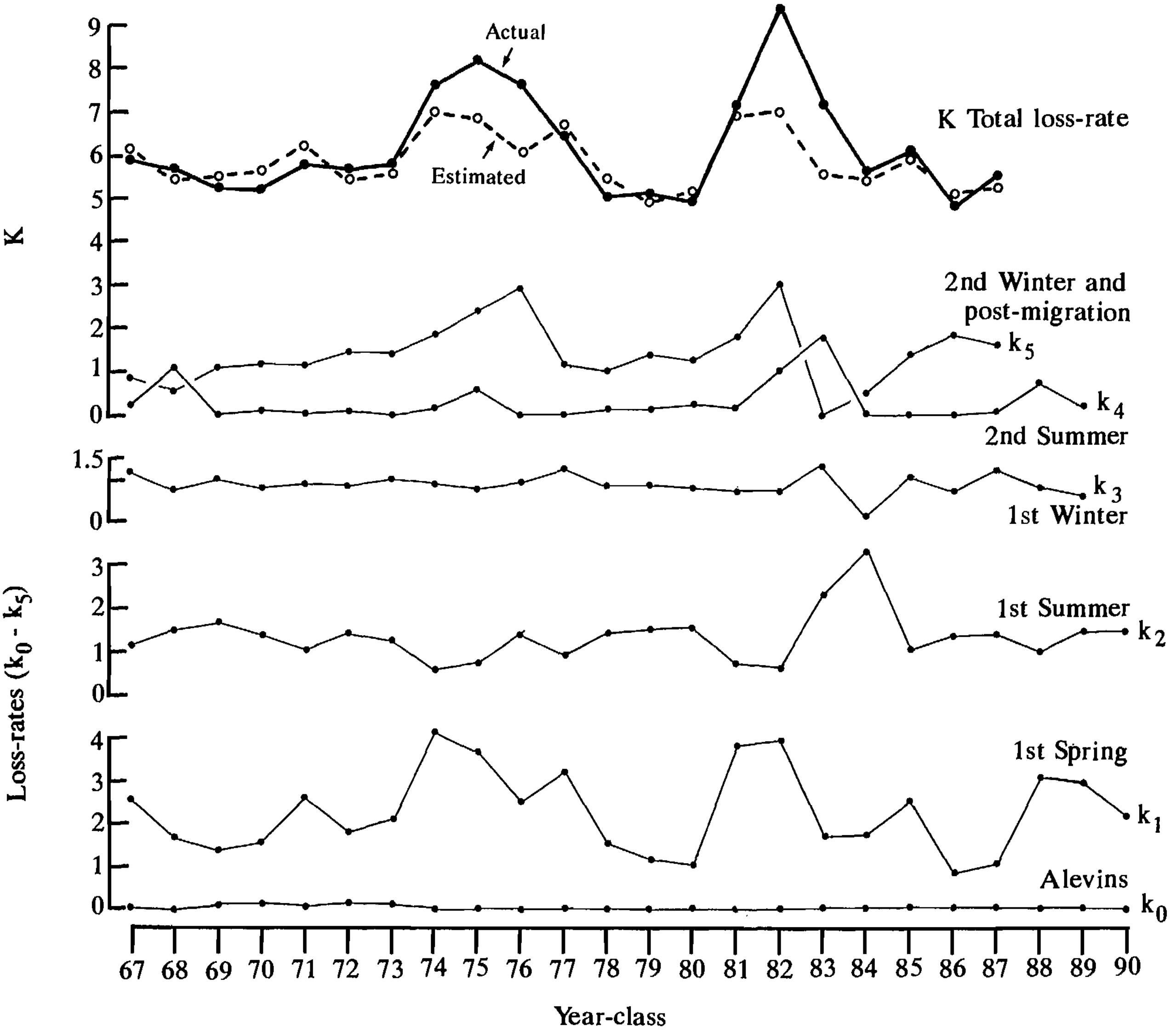

FIG. 3. Relationship of various loss-rates (k_0 - k_5) to the total loss-rate (K) for the decrease in numbers between the egg stage and 3+ female spawners in the different year-classes; loss-rates were for the decrease in numbers between egg and alevin stages ($k_0 = \ln(0.5S/0.5R_0) = \ln(S/R_0)$), alevin stage and 0+ parr stage in May/June ($k_1 = \ln(R_0/R_1)$), 0+ parr stages in May/June and August/September ($k_2 = \ln(R_1/R_2)$), 0+ parr stage in August/September and 1+ parr stage May/June ($k_3 = \ln(R_2/R_3)$), 1+ parr stages in May/June and August/September ($k_4 = \ln(R_3/R_4)$), 1+ parr stage in August/September and 3+ females in November/December ($k_5 = \ln(0.5R_4/R_5)$; for total loss-rates (K), actual values (●) are compared with values (○) estimated from equation (4b) with $\hat{a} = 4.767$ and $b = 0.000297$.

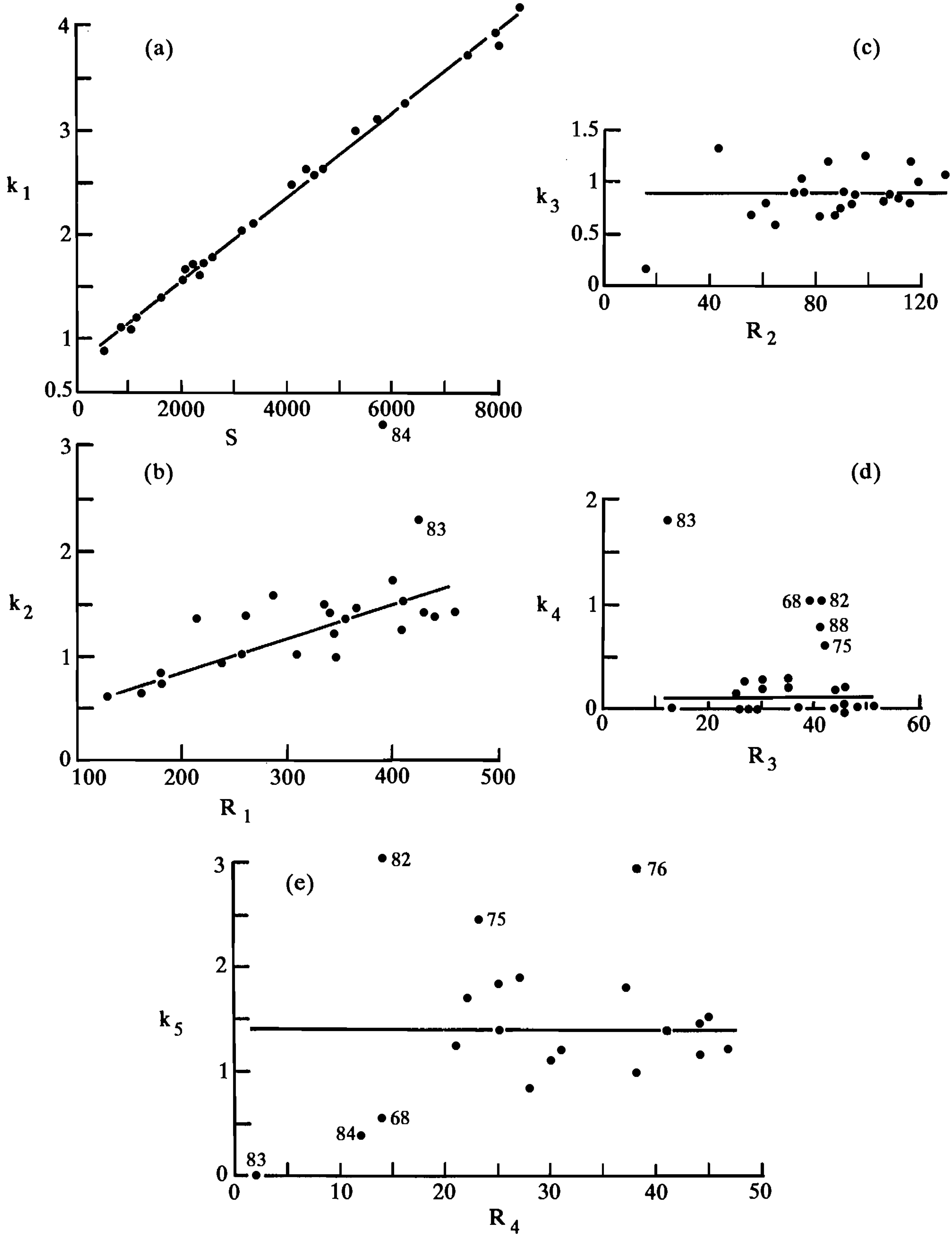

FIG. 4. (a)–(e). Relationship between each loss-rate (k_1 - k_5) and the initial density (S and R_1 - R_4) for the period over which the loss-rate was estimated; linear regression lines: $k_1 = a + bS$ where a (with 95% C.L.) = 0.698 ± 0.0733, b(with 95% C.L.) = 0.000415 ± 0.0000162, $r^2 = 0.993$ (P<0.001) for relationship between k_1 and S; $k_2 = a + b\ R_1$ where a (with 95% C.L.) = 0.429 ± 0.350, b (with 95% C.L.) = 0.00245 ± 0.00108, $r^2 = 0.542$ ($P<0.05$) (values for 1983 and 1984 excluded from analysis); regressions for relationships between k_3 and R_2, k_4 and R_3, k_5 and R_4 were not significant ($P>0.05$) and therefore the horizontal lines are arithmetic means for k; k_3 (with 95% C.L.) = 0.880 ± 0.116, k_4 = 0.102 ± 0.053 (excluding values for 1968, 1975, 1982, 1983, 1988) k_5 = 1.424 ± 0.360.

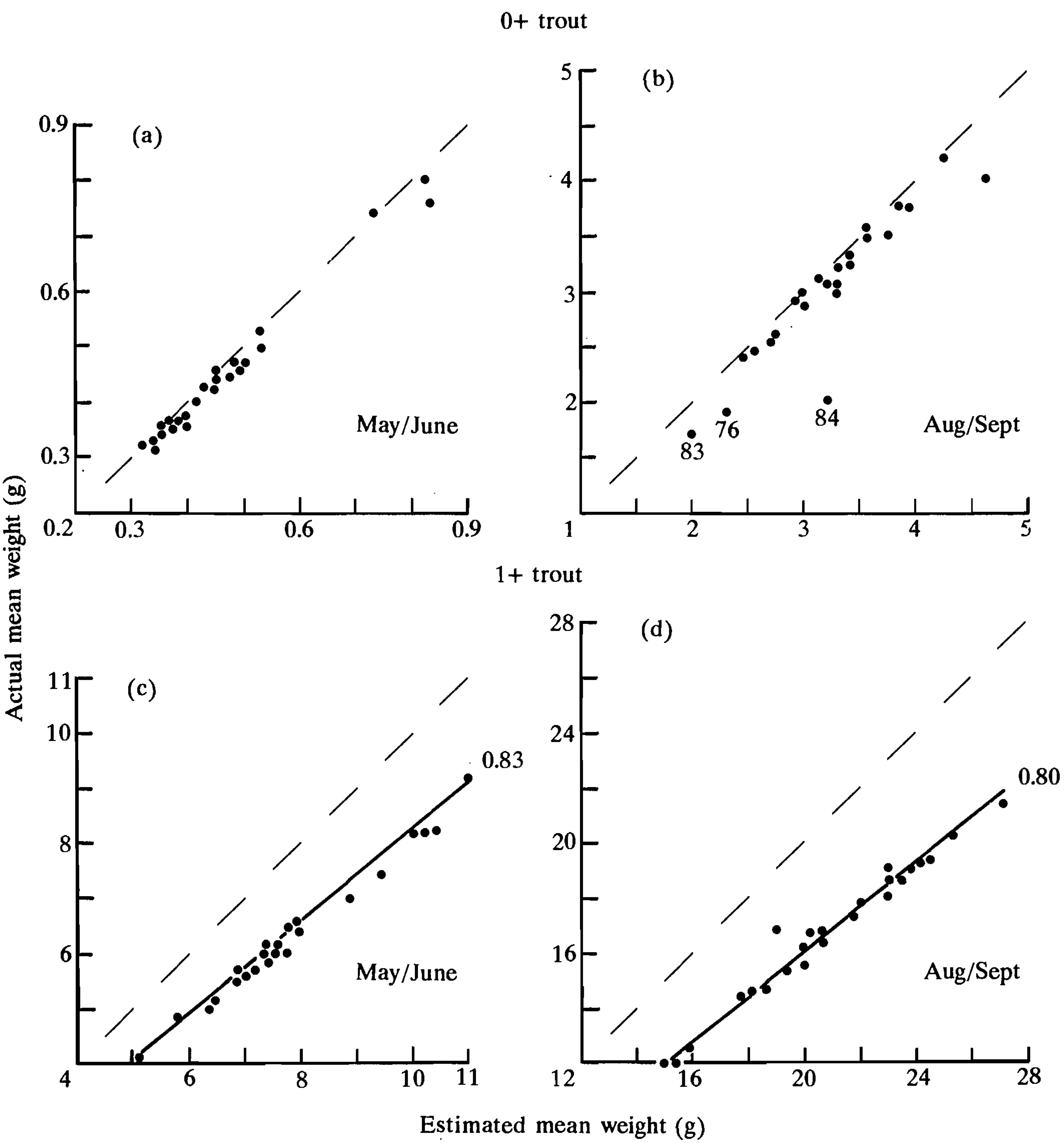

FIG. 5.Comparisons between actual mean weights (g) and values estimated from equation (5) for: (a) 0+ trout in late May/early June; (b) 0+ trout in late August/early September; (c) 1+ trout in late May/early June; (d) 1+ trout in late August/early September (broken line indicates equality, solid line is mean ratio for actual value/estimated value).

Equation (4a) could therefore be reduced to the simpler form of equation (4b) which was then used to estimate K for each year-class. Most estimated values from this simple model (open circles in Fig. 3) were very similar to actual values (closed circles), the major exceptions being the 1975, 1976, 1982, 1983 year-classes that were affected by the summer droughts of 1976, 1983, 1984.

These analyses showed that population density throughout the life cycle was regulated chiefly by density-dependent survival in the early life-stages, the key-factor being the spring losses soon after the

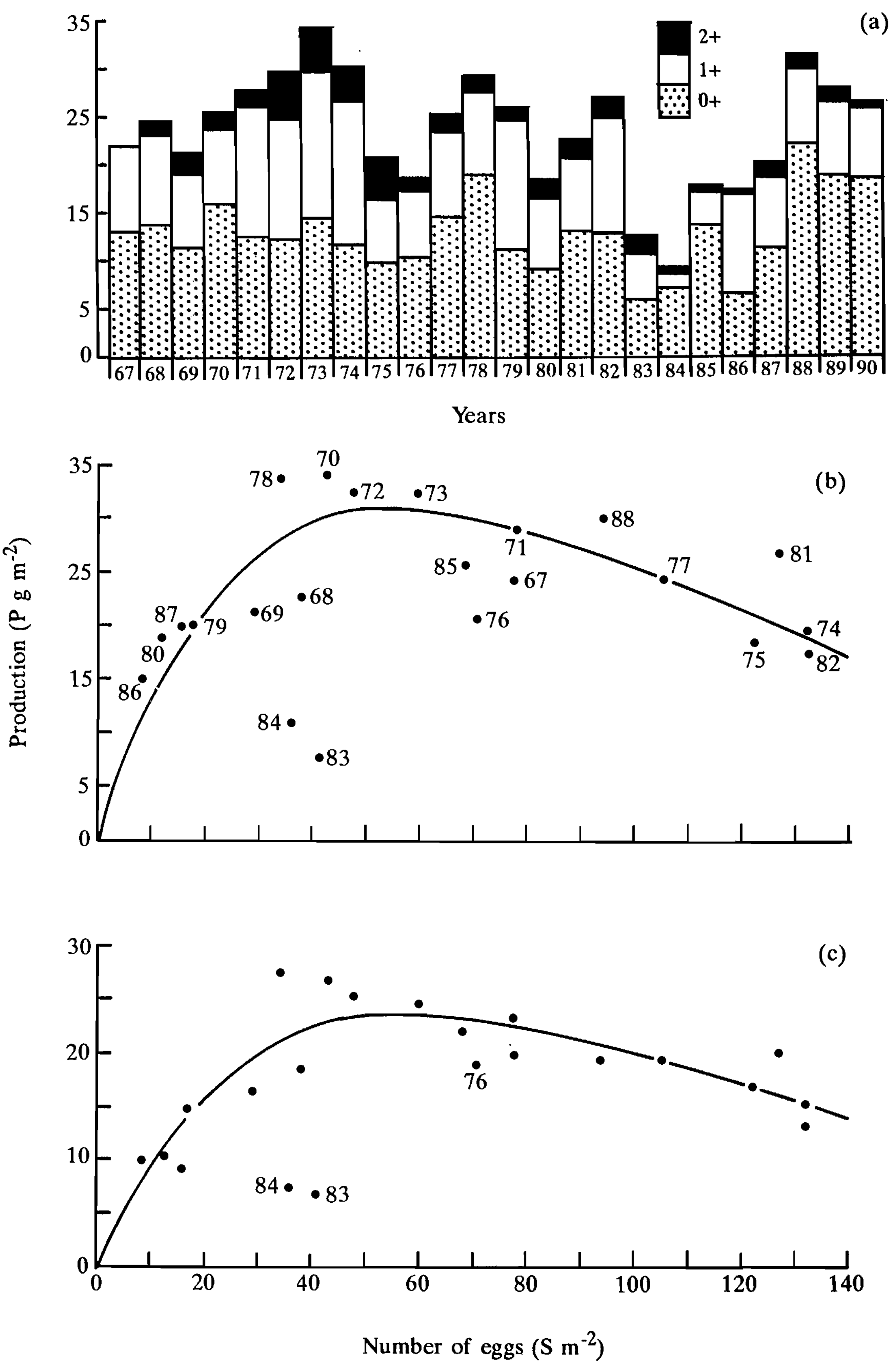

Fig. 6. (a) Total production of trout in each year (Pg m^{-2}) for the freshwater phase of the life cycle (contributions by different ages of trout are shown by different shading, see key on figure); (b) Relationship between total production of trout in each year-class (Pg m^{-2}) for the freshwater phase and mean number of eggs at the start of each year-class (S eggs m^{-2}), curve was estimated from equation (1) with P substituted for R and $\hat{a}$ = 1.526 (SE 0.119) and b = 0.0179 (SE 0.00107), r^2 = 0.567 ($P<0.001$) (year-classes are indicated but those for 1976, 1983, 1984 were excluded from analysis); (c) Relationship between total production in each year-class (Pg m^{-2}) and initial egg density (S eggs m^{-2}) with P values corrected for the effect of live weight (Wg) of 2+ trout on 30 April, curve was estimated from equation (7) with a = 1.111 (SE 0.189), b = 0.0170 (SE 0.0011), c = 12.52 (SE 6.48), d = 0.461 (SE 0.146) r^2 = 0.742 ($P<0.001$) (1976, 1983, 1984, values excluded from analysis).

young trout emerged from the gravel and started to feed. Apart from a few year-classes affected by three severe droughts, the total loss-rate between the egg stage and female spawners was estimated by a very simple model (equation 4b).

Growth

The adequate fit of the growth model (equation 5) to different life stages in most year-classes (Fig. 5) showed that growth was not density-dependent but was affected chiefly by water temperature, a secondary factor being the size of the newly emerged fry. There was excellent agreement between actual mean weights and estimated values for 0+ trout in late May/early June and in late August/early September (Fig. 5a,b), apart from three very low values at the end of the summer droughts of 1976, 1983, 1984. Although these same droughts had no obvious effects on growth rates in the second summer of the life cycle, actual weights for 1+ trout rarely exceeded about 80% of the estimated values on both sampling occasions (Fig. 5c,d). The slightly lower actual weights were due to depressed growth in the first winter of the life cycle because growth rates in the second summer were close to maximum values (Elliott 1985c).

Additional samples for other stages in the life cycle were taken in some year-classes and confirmed the reliability of the growth model (Elliott 1985c). It was therefore used to estimate the mean wet weight of third year trout (age 2+ years) on 30 April. This date was close to the end of the freshwater phase of the life cycle; most 2+ trout started to migrate downstream as smolts in May and eventually reached the sea/estuary in summer (Elliott 1985a). Estimated values were used in the analysis of the production estimates, using equation (8).

Production

Annual production varied considerably over 24 years with an overall mean value of 23.40 g m^{-2} (SE 1.23) and a range of 8.86–33.90 g m^{-2} (Fig. 6a). Production was always lowest for third year trout (age 2+ years), highest for 1+ fish in six year-classes (1971–74, 1979, 1986) and highest for 0+ fish in the remaining eighteen year-classes. The lowest annual production rates were associated with the drought years of 1983, 1984, but the effect of the 1976 drought was less marked.

Total production for each year-class also varied considerably over 22 year-classes with a mean value of 23.00 g m^{-2} (SE 1.53) and a range of 7.59–33.88 g m^{-2} (Fig. 6b). When the three year-classes associated with severe droughts (1976, 1983, 1984) were excluded from the analysis, equation (1) was a good model for the density-dependent relationship between year-class production and the number of eggs at the start of each year-class. The r^2 value indicated that density-dependent survival could explain 57% of the variation in production between year-classes.

When the estimates of mean weight of 2+ trout on 30 April were included in the analysis, using equation (7), the improved fit of the model indicated that density-independent growth accounted for an additional 17.5%.

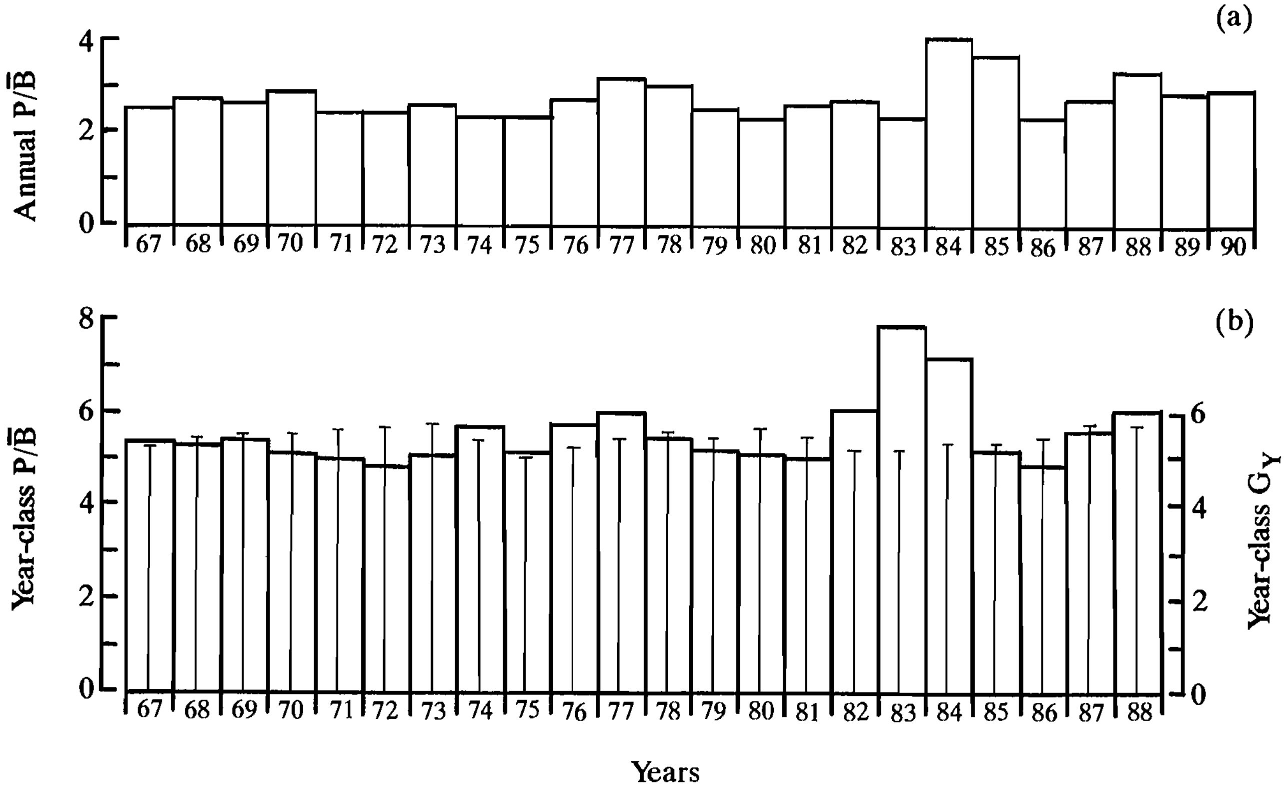

Fig. 7. (a) Annual production to mean biomass ratios (P/B) from 1967 to 1990. (b) Year-class production to mean biomass ratios (P/B) from 1967 to 1988 (columns), and year-class instantaneous growth rate (G_y) for the same period (single lines within each column).

The new model therefore shows that the combined effects of density-dependent survival and density-independent growth could account for 74% of the variation in production between year-classes (Fig. 6c).

The annual production to mean biomass ratio (*P/B*) varied slightly (CV 16%) over 24 years with an overall mean value of 2.73 (SE 0.0910) and a range of 2.28–4.02 (Fig. 7a). The year-class production to mean biomass ratio was slightly less variable (CV 13%) over 22 year-classes with a mean value of 5.53 (SE 0.158) and a range of 4.78–7.83 (Fig. 7b). Comparisons were made between the year-class *P/B* values and the natural logarithm of the ratio of mean wet weight of 2+ trout on 30 April (W_s g) and mean wet weight of newly emerged fry at the start of the year-class (W_0 g). The latter value is, of course, the year-class instantaneous growth rate (G_y) for the whole freshwater phase of the life cycle. It should be theoretically equal to the year-class *P/B* ratio, and in many years the two values were very similar (Fig. 7b). Year-class G_y was less variable (CV 3%) than year-class *P/B*, and had a mean value of 5.41 (SE 0.0367) over 22 year-classes with a range of 5.10–5.70. Possible reasons for the discrepancies between year-class *P/B* and year-class G_y will be discussed later.

Discussion

Population Density and Survival

The population density of the juvenile sea-trout in Black Brows Beck is regulated chiefly by density-dependent survival in the early life-stages. Recent work has shown that there is a critical period for survival during the fry stage soon after the young trout emerge from the gravel nest and start to feed (Elliott 1989d,e, 1990a,b). The critical period varies between year-classes (range 33–70 days after fry emergence) and is itself inversely density-dependent on egg density.

Survivor density and loss-rates are strongly density-dependent on egg density during the critical period, but proportionate survival with stable loss-rates occurs after it, as also shown by the key-factor analysis for the later life-stages (Fig. 3, 4). Selection intensity for territorial fish, and hence mortality, is also highest during the critical period and is both density-dependent and size-dependent; the size distribution of the fish being trimodal, bimodal and unimodal at low to medium, relatively high and very high egg densities, respectively.

Although Bachman (1984) has suggested that agonistic behaviour in salmonids results in the establishment of dominance hierarchies and gives the false impression of territoriality, other workers have concluded that salmonids are territorial in streams, especially the juvenile fish (e.g., Onodera 1967; Chapman and Bjornn 1969; Jenkins 1969; Noakes 1978; Grant, et al. 1989). Individual fish maintain a feeding station, the optimum stations being those that are the most energetically profitable (e.g., Fausch 1984; Metcalfe 1986; Godin and Rangeley 1989).

For the juvenile sea-trout in Black Brows Beck, territorial possession and the size of territorial fish provide the link between density-dependent survival, selection intensity and size-dependent mortality (Elliott 1990b). Territorial size and defence are chiefly related to fish size but as egg density and the number of trout without territories increases, the time spent defending a territory increases. At high densities of trout without territories, the largest territorial trout could spend up to 55% of their time in territorial defence and the time left for feeding would be probably insufficient to obtain an adequate energy intake. Increasing defence costs are therefore probably responsible for the elimination of larger juveniles at high initial egg densities, and for increasing selection intensity for an optimum size of trout during the critical period. The mechanisms responsible for population regulation in juvenile sea-trout are therefore now clearer and can be used to improve the mathematical models used to describe the complex processes responsible for fluctuations in population density and survival.

The models summarised in equations (1), (2) and (4) are inadequate for year-classes affected by severe summer droughts, especially those in 1976, 1983, 1984. In all cases, loss-rates were higher, and survival rates lower, than expected (Fig. 1, 3, 4). The complete generation relationship between eggs produced by surviving progeny and initial egg density in each year-class showed that only the 1983 year-class was affected markedly by the droughts (Fig. 2). This is probably because the 1983 year-class was the only one to experience two successive summer droughts in 1983 and 1984.

A stability analysis at the equilibrium point of 79 eggs m^{-2} (*S** on Fig. 2a) indicates that population density in Black Brows Beck is essentially stable. Equilibrium theory postulates that after a perturbation, the population density will eventually return, after some oscillations, to the equilibrium density of 79 eggs m^{-2}. Such stability may be partially responsible for the high production rates for the juvenile sea-trout. However, severe and frequent perturbations, such as repeated droughts, could soon increase the gradient at the equilibrium point and a stable population could rapidly change to first cyclic, and then chaotic, fluctuations in density with eventual extinction. One of the many advantages of long-term studies is that they provide early warning of such changes in stability before it is too late.

Growth

The model (equation 5) shows that both mean weight and mean growth rate are density-independent and chiefly affected by water temperature (Fig. 5). Severe summer droughts in 1976, 1983, 1984 retarded growth in the first, but not the second, summer of the life cycle. The poor growth of these year-classes is probably chiefly responsible for their poor production rates.

Although mean sizes and growth rates were unaffected by population density, the latter did influence variation in individual size in Black Brows Beck. Relative variation in size was fairly constant for newly emerged fry but was inversely related to egg density throughout the rest of the life cycle (Elliott 1984b, 1985c,d). Comparisons between laboratory reared siblings and field data for the same year-classes provide strong evidence that the changes in size variation in the field are due to natural (stabilizing) selection rather than other mechanisms such as sampling bias or developmental canalization (Elliott 1989a). As already mentioned, selection intensity with size-dependent mortality is highest during the critical period so that as egg density increases, the number of modes in the size distribution of the fish decreases from three to one (see also Elliott 1990a). Such changes in modality could clearly affect estimates of production and mean biomass, and could account for some of the variation unexplained by the model summarised by equation (7), i.e. some of the missing 26%!

Production

The values for annual production in Black Brows Beck are higher than those given for most salmonid streams (e.g., Randall and Paim 1982; Jankov 1986; Mann and Penczak 1986; Penczak et al. 1986; Randall and Chadwick 1986; Rasmussen 1986; Williams and Harcup 1986; Gibson 1988; Kelly-Quinn and Bracken 1988; Waters 1988; Newman and Waters 1989; Bergheim and Hesthagen 1990; Waters et al. 1990). Examples of high values comparable to those of the present study are 12.2–36.0 g m^{-2} for brown trout in a North American stream (Brynildson and Brynildson 1984) and 14.1–33.1 g m^{-2} for brown trout in different sections of a Danish stream (Mortensen 1978). The high production rates in Black Brows Beck are undoubtedly due to the large contributions of fish in the first and second years of their life cycle (Fig. 6a). A migratory strategy ensures that larger trout do not use resources such as food and space. These older fish remain in other non-migratory trout populations to form a major part of the biomass whilst contributing little to production and reducing the resources available to young trout.

Annual $P/\bar{B}$ ratios for the juvenile sea-trout in Black Brows Beck (Fig. 7a) are also higher than most values given in the literature (see references above). The simplest explanation is once again the fact that all the trout are juveniles. Similar high ratios have been obtained in some nursery streams for other migratory salmonids (e.g., Chapman 1965; Hopkins 1971). Year-class $P/\bar{B}$ ratios (equivalent to cohort $P/\bar{B}$ ratios for invertebrates) are slightly less variable than annual $P/\bar{B}$ values, and most values lie in the range 5–6, which is also the range suggested for benthic invertebrates by Waters (1987). Year-class $P/\bar{B}$ ratios and instantaneous growth rates (G_y) are very similar in most year-classes (Fig.7b). The major exceptions with $G_y < P/\bar{B}$ are for the 1982, 1983, 1984, year-classes, all of which were affected by the summer droughts of 1983 and 1984. In these year-classes, there were periods of very high mortality and poor growth, both of which caused low productivity but even lower mean biomass. As Ricker (1946) first recognised, $P/\bar{B}$ equals G_y only if growth and mortality rates are exponential. It is therefore surprising that there were so few major discrepancies between $P/\bar{B}$ and G_y in the 22 year-classes.

Most previous estimates of production rates in salmonid streams are based on data collected over less than 5 years. The present investigation over 25 years shows that both annual and year-class production can vary considerably between years. Many of the estimates for different salmonid species in a wide range of localities would fit within the range of 8.86–33.90 g m^{-2} for annual production in Black Brows Beck.

The model (equation 7) shows that 74% of the variation in production rates between year-classes could be explained by the combined effects of density-dependent survival and density-independent growth (Fig. 6b,c). Once again, the three year-classes most affected by the severe droughts of 1976, 1983, 1984 had to be excluded from the analysis. Of the two factors affecting production rates, density-dependent survival was clearly the most important. The mechanisms responsible for density-dependent survival have already been discussed and could be used to improve the production model as well as the original models for population density and survival.

This long-term investigation has therefore shown that realistic mathematical models can be constructed to describe the complex processes that affect production rates. All the models could be, and will be, improved. Such models are essential tools for the conservation and management of the fish stocks and can be used to predict the optimum fish density in different populations, the maximum attainable growth and production in different habitats and the effects on trout populations of environmental changes due to natural causes (e.g. droughts, spates) or human activities. Long-term studies are essential for the development of these models but, unfortunately, it is becoming increasingly difficult to obtain support for such work.

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Juvenile Salmon Stock Assessment and Monitoring by the National Rivers Authority — A Review

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The National Rivers Authority (NRA) is responsible for the management of salmon fisheries in England and Wales comprising over 70 principal river catchments which support valuable and important recreational, and in many cases commercial, salmon fisheries. The effective management of these populations and their fisheries requires the assessment of their status and those factors which influence their distribution and abundance. In the Welsh Region of the NRA, since 1985 a strategic approach has been adopted for assessing juvenile salmon stocks which involves annual sampling at key sites targeted on catchments supporting major fisheries, with other catchments being sampled less frequently under a rolling programme. Key sites are selected following an extensive baseline survey and a combination of quantitative and semi-quantitative methods are employed. The results of these surveys are collated and published annually, providing baseline data on fish distribution and abundance as well as trends at key sites. In addition supporting studies have been undertaken into the relationship between the different methods employed and a simple classification system has been developed which aids interpretation and communication of survey results. A predictive model has also been developed relating habitat variables to fish density to aid interpretation of population data.

La National Rivers Authority (NRA) est responsable de la gestion de la pêche au saumon en Angleterre et au pays de Galles; elle couvre plus de 70 grands bassins hydrographiques qui contiennent des pêcheries de saumon précieuses et importantes sur le plan sportif et, dans de nombreux cas, sur le plan commercial. Pour gérer efficacement ces populations et leur pêche, il faut évaluer leur situation et les facteurs qui influent sur leur distribution et leur abondance. Dans la région galloise de la NRA, on a adopté en 1985 une approche stratégique pour l'évaluation des stocks de saumons juvéniles, approche qui fait appel à un échantillonnage annuel sur des sites clés situés dans des bassins où ont lieu les pêches principales, tandis que les autres bassins sont échantillonnés moins fréquemment mais à tour de rôle. Les sites clés sont sélectionnés à la suite d'un relevé général de grande ampleur, et on emploie une combinaison de méthodes quantitatives et semi-quantitatives. Les résultats des relevés sont colligés et publiés annuellement, et ils fournissent des données générales sur la distribution et l'abondance des poissons ainsi que sur les tendances aux sites clés. En outre, des travaux complémentaires ont été entrepris sur la relation entre les différentes méthodes employées, et on a mis au point un système simple de classification qui facilite l'interprétation et la communication des résultats des travaux. Un modèle prédictif a également été élaboré qui met en rapport les variables de l'habitat et la densité des poissons et doit faciliter l'interprétation des données démographiques.

Introduction

The National Rivers Authority (NRA) is responsible for the maintenance, improvement and development of salmon fisheries in England and Wales. The NRA also has statutary duties and powers in relation to water resources, pollution control, flood defence, recreation, conservation and navigation. It is divided into ten operational regions (Fig. 1) based upon catchment boundaries with a national headquarters responsible for overall co-ordination and policy development.

Management of the fishery resource includes the control of both legal and illegal exploitation, improving habitat and fish passage and safeguarding water quality and quantity. It is important to be able to monitor the effectiveness of these management actions; one way is by assessing and monitoring the status and performance of the stock. This paper reviews the use of juvenile salmon stock assessments in the management of salmon fisheries, principally within the Welsh Region of the NRA, and outlines future proposals for a strategic stock assessment programme throughout England and Wales.

The Resource

The fisheries resource in England and Wales is significant and diverse with Atlantic salmon (*Salmo salar* L.) and both migratory and resident brown trout (*Salmo trutta* L.) predominating in the northern and western rivers. Over 70 principal rivers support commercial fisheries or have a mean annual rod catch in excess of 30 salmon or 100 sea trout.

About 900 licensed commercial salmon instruments operate in rivers, estuaries and coastal waters where the numbers are mainly limited by order; the gear type, season and use are also strictly regulated using byelaws. Total commercial catches of salmon in England and Wales have averaged 75,271 fish annually since 1985.

Angling for salmon is a popular and economically important recreation, with around 40,000 licences issued in 1989. Byelaws govern the methods and

FIG. 1. Regions of the National Rivers Authority.

season for angling, and total rod catches of salmon in England and Wales have averaged 21,447 fish annually since 1985.

Juvenile Stock Assessment Methodologies

The relationship between the number of adults and the number of progeny produced is complex (Solomon 1985) and direct enumeration of adults can be both difficult and costly. Current knowledge is generally derived from two main sources; extensive data on catches and the distribution and abundance of juveniles in freshwater. Due to the large flow variations and high debris load of many of the salmon rivers, the trapping and enumeration of smolts is an applicable technique only for specific research purposes.

Surveys of juvenile salmonid populations are routinely carried out for a variety of reasons using various methodologies and strategies. The status of these populations can be used as an index of the quality of the freshwater environment and of the effectiveness of measures to improve both the environment and the management of the fisheries resource itself.

Many factors affect the well-being of salmon stocks; some operate in a random fashion outside any direct control by management. The interpretation of information on fish distribution and abundance requires an extensive database which takes into account both spatial and temporal variations in these parameters.

Information on the distribution and abundance of fish stocks in small rivers and streams has been obtained commonly using standard run-depletion 'quantitative' electric-fishing surveys at a limited number of sites (Strange et al. 1989). These data provide detailed information on fish stocks at specific sites for one point in time and are important when precise numerical information is required, e.g., production estimates or detailed impact assessments. Since it is generally not possible to sample entire stream lengths, it is necessary to sample discrete sites. This strategy requires an extension of the site results to the rest of the stream and so the study design, i.e., number and location of sites, must allow such an extension to be made on a statistical basis.

However, for broader catchment management purposes an overview of the status of the juvenile stock is often all that is required and these 'quantitative' results have been of restricted value since they can be time- consuming to collect and may be unrepresentative of the catchment as a whole. Methods which allow a larger number of sites to be sampled for the same manpower but which still retain an acceptable level of accuracy are therefore of value. Two such sampling techniques have been employed in the Welsh Region.

The first, a semi-quantitative method, involves carrying out a single sampling count over an un-netted, measured area of stream (typically 30 m long). This method was evaluated by carrying out a standard quantitative population estimate at the same sites covering a range of fish densities and habitat types in streams up to 10m wide (Strange et al. 1989). The relationship between the count and the standard estimate (Fig. 2) was examined, and the relatively high proportion of explained variation for the relationship between the $\log_{10}$ n+1 transformed results ($r^2 = 0.864$ and 0.785 for 0+ and >0+ salmon respectively) enables predictions to be made. The semi- quantitative count increases with increased population densities.

Since this relationship is not without variation, a categorisation system has been developed with descriptive classes reflecting the status of stocks. Data from both sources are similarly treated, thus enabling comparison between a variety of sites using the count or the estimate (Fig. 3). Based upon this rationale, a categorisation system was devised (Table 1a and 1b) with the class boundaries approximately corresponding to percentiles based upon the frequency distributions of salmon densities from rivers in the Welsh Region. Fry (0+) and parr (>0+) densities are each assigned to a category and the two are then combined into a single A to E classification. The combination of age-classes in the matrix is an attempt to reduce the effect of site-specific habitat; thus a site with habitat which is poor for only one of the two age-groups will not be downgraded. Management action is triggered by either a decline in category between years or if categorised in classes D or E. This approach allows a relatively simple, easily communicated overall assessment of the status of juvenile stocks to be made, and areas of concern are targeted for more intensive investigation.

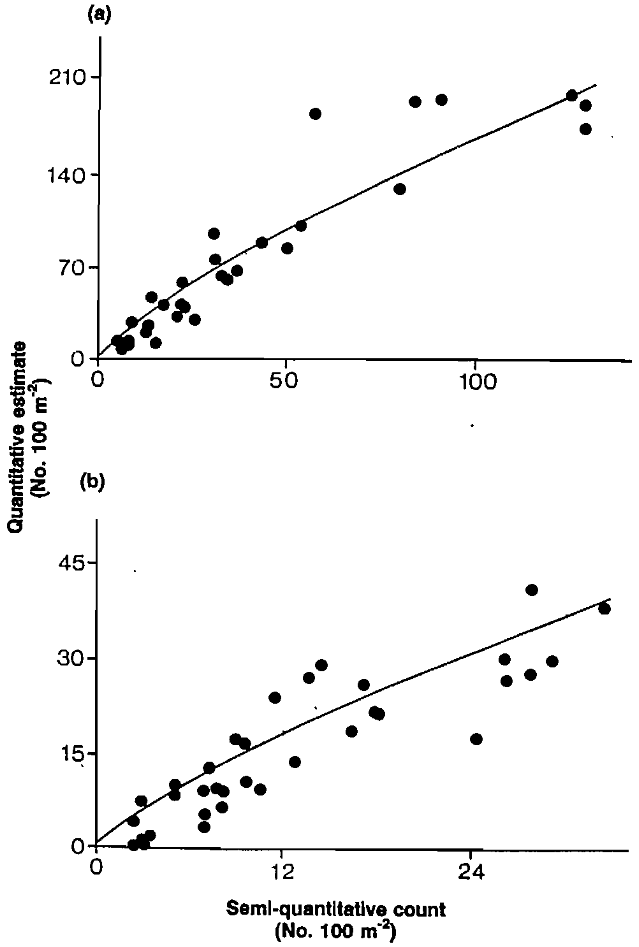
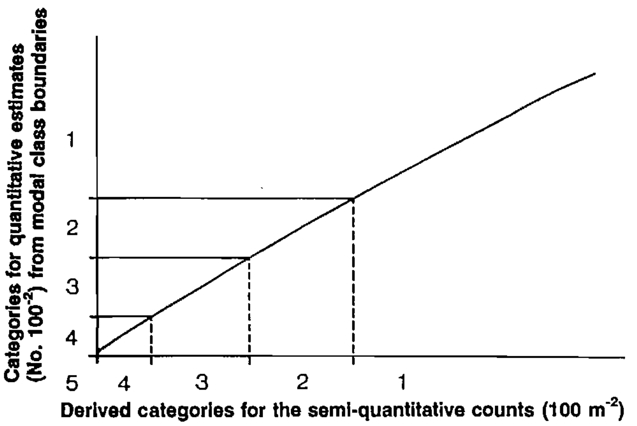


FIG. 2. The arithmetic relationship between the quantitative estimates and semi-quantitative counts (no. 100 m^{-2}) for 0+ (a) and >0+ (b) salmon parr with the linearised log $10n + 1$ regression fitted: (a) $y + 1 = \text{antilog } 0.667\ (x + 10.779)$, and (b) $y + 1 = \text{antilog } 0.405\ (x + 10.787)$.

TABLE 1a. Abundance categories (numbers 100 m^{-2}) for juvenile salmon

	Method			
	Quantitative		Semi-Quantitative	
	Fry(0+)	Parr(>0+)	Fry(0+)	Parr(>0+)
Excellent	>100	>25	>50	>20
Good	50.01–100	15.01–25	22.51–50	10.01–20
Moderate	25.01–50	5.01–15	10.01–22.5	2.26–10
Poor	0.01–25	0.01–5	0.01–10	0.01–2.25
Absent	0	0	0	0



KEY: 1. Excellent, 2. Good, 3. Moderate, 4. Poor, 5. Absent.

FIG. 3. Categorisation of results using the fitted lineraised log $10n + 1$ regression $y + 1 = \text{antilog } a\ (x + 1^b)$ to derive boundaries from modal class distribution.

The second semi-quantitative method is targeted on fry counts in shallow, riffle areas. The number of fish captured, plus those observed but not caught, during five minutes sampling time is used as an index of fry abundance (Kennedy 1981). These counts are used for both spatial and temporal comparisons, particularly in wide rivers where quantitative sampling is difficult and often impossible.

Habitat Assessment

The carrying capacity of a stream can vary considerably and is to a large extent dependent on channel structure and the hydrological, chemical and temperature regimes. In Welsh Region, a system for measuring and evaluating stream salmonid habitat features called HABSCORE has been developed. It is based on empirical statistical models which are species and age-specific and relate predicted fish populations to observed habitat variables recorded on a standard questionaire form. Habitat features including width, depth, substrate, flow, cover, land use and riparian vegetation are recorded. Catchment data such as altitude, gradient and catchment area are measured from 1:50,000 scale maps. These data are entered onto a computer spreadsheet which drives five statistical models which have been built for salmon (0+ and >0+) and trout (0+, >0+ (<20cm) and >20cm). Observed densities from electric- fishing surveys can also be entered onto the spreadsheet.

Two new parameters are produced by the HABSCORE models. Habitat Quality Score (HQS) is a measure of the habitat quality expressed as the

TABLE 1b. Classification matrix for juvenile salmonids

		FRY(0+)				
		Excellent	Good	Moderate	Poor	Absent
PARR(>0+)	Excellent	A	A	A	B	C
	Good	A	A	B	B	C
	Moderate	A	B	B	C	D
	Poor	B	B	C	D	D
	Absent	C	C	D	D	E

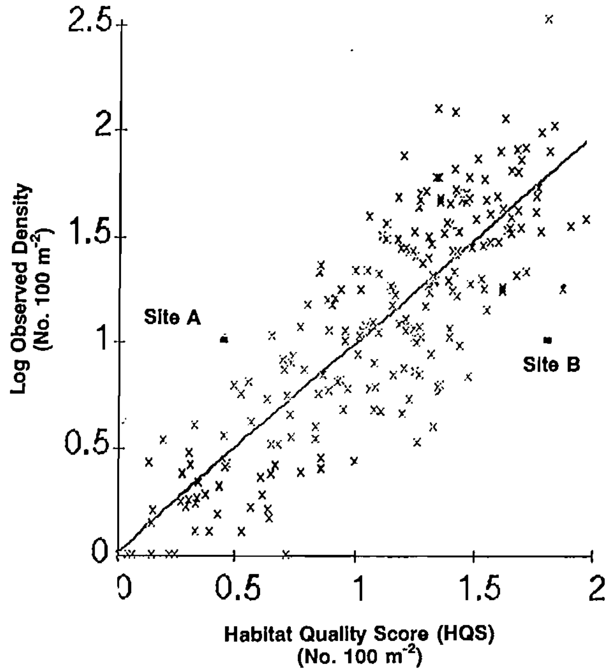


FIG. 4. Habscore trout fry model relationship.

expected density of fish under pristine conditions where water quality or recruitment are not limiting. Confidence limits for the HQS are also calculated. The Habitat Utilisation Index (HUI) is a measure of how the observed density compares with the expected density (HQS) and low values indicate a statistically significant departure from that expected.

The model for trout fry (Fig. 4) demonstrates the importance of evaluating habitat when assessing the status of populations. Site A and site B have the same observed density of trout fry; however, the expected density at site B is significantly higher, indicating that one or more factors is severely limiting trout fry abundance at this site.

Future Juvenile Salmonid Stock Assessment

The NRA has recently formulated a strategy for fish stock assessment in England and Wales which encompasses juvenile salmon (NRA 1991). Since 1985 a monitoring programme for juvenile salmonids has been carried out in Welsh Region to establish a baseline of information on the distribution and abundance of juvenile salmonid stocks and to monitor any changes in relation to natural and management-based factors.

In Welsh Region over 50 river catchments support salmonid populations amounting to over 20,000 km of streams of which around 7,000 km are available to salmon. With limited manpower resources, annual sampling of representative key sites (selected from an initial extensive baseline survey) is targeted at a number of major catchments which support significant fisheries. Other catchments are sampled less frequently under a rotating programme. Typically each year about 20 catchments are sampled comprising about 120 quantitative sites, 300 semi-quantitative sites and 100 riffle sites.

A strategic approach to stock assessment is being proposed for the NRA with the method, type of data collected and the precision level related to the aim of the survey (Bohlin 1990). The manpower requirement to introduce this strategic programme is currently being assessed so that the necessary resources can be obtained.

In addition, the NRA has commissioned further research into the application of HABSCORE to a wider range of river types so that it can become a standard habitat evaluation technique. Further, a fisheries classification system is being developed based on a hierarchical, modular structure which will allow it to be flexible enough to be applied to a number of different uses and to be used at different levels of complexity.

In the past, many stock assessments were reactive with surveys carried out to investigate a particular problem. This approach resulted in a lack of consistent monitoring of juvenile salmon populations in England and Wales and a scarcity of baseline information. The approach now being adopted by the NRA should enable these inconsistencies to be overcome and provide data to enable salmon populations to be managed more effectively.

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Influence des paramètres hydromorphologiques sur l'utilisation de l'habitat par les juvéniles du Saumon atlantique (*Salmo salar*)

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Les principaux habitats fluviatiles du Saumon atlantique juvénile de la Côte-Nord du Québec peuvent être catégorisés par la photo-interprétation en fonction du faciès d'écoulement et de la granulométrie, selon les catégories suivantes: chenal, rapide, seuil et bassin. Afin d'optimiser les valeurs de production relatives attribuées à ces habitats, il convenait de préciser le potentiel qu'ils offrent aux juvéniles de divers âges.

À partir des données de la rivière de la Trinité, il est démontré, par analyse factorielle des correspondances, que les alevins utilisent préférentiellement les seuils et les chenaux, alors que les rapides sont utilisés surtout par les tacons. Aucun groupe d'âge n'utilise préférentiellement les zones des bassins de moins de 1,5 m de profondeur soumises à l'inventaire. La même méthode d'analyse montre que la vitesse du courant, la profondeur et la granulométrie n'influencent pas cette utilisation préférentielle des habitats, mais viennent moduler la taille des individus présents. Ainsi, dans les seuils, les alevins de petite taille sont associés aux vitesses et aux profondeurs faibles. Dans les rapides, l'augmentation du diamètre moyen du substrat se traduit pas une présence accrue des grands tacons. Les résultats d'une analyse en composantes principales montrent que les paramètres vitesse, profondeur et granulométrie expliquent une proportion constante, d'une année à l'autre, de l'utilisation de l'habitat par les juvéniles sur la rivière de la Trinité.

Through aerial photo analysis, the major juvenile Atlantic salmon river habitats of Quebec's North Shore can be classified by flow regime and riverbed morphology and substrate, according to the following categories: channels, runs, riffles and pools. In order to optimize the relative production values attributed to these habitats, it is necessary to specify the potential that they offer to the various age groups of young salmon.

From the data obtained from the *rivière de la Trinité* it has been shown (by factorial correspondences analysis) that fry prefer riffles and channels, whereas, parr mostly prefer runs. Sampled area of less than 1.5 m deep in pools are not preferred by any age group in particular. The same method of analysis also shows that neither the water velocity nor depth and substrate have an influence on habitat preferences but affect rather the size of the individuals. For example, in riffles, small fry are associated with low water velocity and shallow depth. In runs, the larger the average substratum diameter, the greater is the number of big parr. The results of a principal component analysis applied on successive years show that water velocity, depth and substrate explain a constant proportion of utilisation of a given habitat by juvenile salmon in the *rivière de la Trinité*.

Introduction

La photo-interprétation a permis de réaliser des progrès importants dans l'évaluation du potentiel des rivières à Saumon atlantique (*Salmo salar*) du Québec. Cette technique permet, à partir de photographies aériennes, de segmenter un cours d'eau en différents faciès d'écoulement: chenal, rapide, seuil, bassin, lac, estuaire, chute, cascade, fosse et frayère (Boudreault, 1984; Clavet, 1980; Dubois et Clavet, 1977).

On procède ensuite de façon empirique à l'évaluation du potentiel salmonicole de chaque segment identifié par la photo-interprétation. Cette évaluation est obtenue en combinant les appréciations de qualité portées sur le faciès d'écoulement et sur la granulométrie de chaque segment. On en arrive ainsi à classer l'habitat du saumon juvénile, sans égard au stade de développement de celui-ci, en trois catégories: très favorable (cote I), favorable (cote II) et peu favorable (cote III). Généralement, les seuils et les rapides sont considérés comme très favorables, les chenaux et les bassins comme favorables et les autres habitats (estuaire, méandre, etc.) comme peu favorables. Ces évaluations du potentiel salmonicole servent soit à estimer la production potentielle de saumonneaux d'une rivière, soit à estimer le nombre d'oeufs requis pour assurer la pleine utilisation de l'habitat en rivière (Côté *et al.*, 1987a, Côté *et al.*, 1987b).

Les différents habitats offrent-ils des potentiels similaires pour différents stades de juvéniles (alevins, petits et grands tacons), et sinon, cela se traduit-il par une utilisation préférentielle? Par ailleurs, quelle est l'influence de la vitesse du courant, de la profondeur et de la granulométrie sur l'utilisation des différents habitats par les juvéniles? Différents auteurs se sont intéressés à ces questions (Jones 1975, Symons et Heland, 1978, Belzile *et al.*, 1982, DeGraaf et Bain, 1986; Morantz *et al.*, 1987; Heggenes et Saltveit, 1990), mais sans qu'on ait considéré globalement le complexe juvénile-habitat-paramètres hydromorphologiques.

Afin de réaliser une telle approche globale et, éventuellement, améliorer les évaluations de potentiels salmonicoles de la photo-interprétation, une étude faisant l'objet de cet article a été produite à partir des captures de juvéniles effectuées par la pêche à l'électricité sur la rivière de la Trinité au Québec. Cette approche intégrée a été concrétisée par une analyse factorielle des correspondances, laquelle permet d'examiner l'influence des paramètres hydromorphologiques sur les juvéniles tout en conservant la structure écologique éventuellement imposée par les types d'habitat.

Matériel et méthode

a) Milieu à l'étude

Les données de cette étude proviennent de la rivière de la Trinité, sur la Haute-Côte-Nord. Cette rivière draine un bassin de 562 km², à même une assise rocheuse granitique. Elle coule sur une distance de 60 km et est fréquentée par le saumon dans sa totalité. Le lit est composé d'une alternance de rapides et de seuils, entrecoupés de zones à écoulements plus lents comme des bassins et des chenaux. L'habitat des juvéniles représente 21 129 unités de 100 m² et se répartit en 12,3 % d'habitats très favorables, 40,3 % d'habitats favorables et 47,4 % d'habitats peu favorables (Caron et Bolduc, 1991).

b) Définition des faciès d'écoulement

Les définitions du faciès d'écoulement sont celles de Clavet (1982). Un seuil est une portion du cours d'eau où il y a alternance de hauts-fonds et de dépressions. L'écoulement y est turbulent, particulièrement en étiage. La profondeur d'eau est généralement faible (< 1 m). Un chenal est une portion du cours d'eau où la profondeur est constante et où l'écoulement est peu turbulent. Un rapide est une portion de la rivière où l'écoulement est très turbulent et la granulométrie très grossière. Un bassin est une portion de rivière où l'écoulement est calme et la profondeur supérieure à deux mètres, ce qui impose une limite à la technique d'échantillonnage utilisée. Ce faciès se traduit souvent par un élargissement du chenal et la présence de fosses.

c) Description des données utilisées

Cette étude a été réalisée à même les données recueillies sur la rivière de la Trinité de 1986 à 1989. Toutefois, seuls les résultats relatifs à l'année 1988 sont présentés. La banque de données sur cette rivière contient, notamment, le nombre de juvéniles capturés par la pêche électrique sur des parcelles de 100 m², la longueur totale des individus capturés et, pour un sous-échantillon, l'âge obtenu par la lecture des écailles. La pêche dans les parcelles est pratiquée de façon systématique à l'aide d'un appareil de marque Coffelt BP1C, en station ouverte ou fermée. Les stations fermées sont d'abord entourées d'un filet pour empêcher l'immigration et l'émigration des poissons, puis on y pêche de 3 à 5 reprises avec une attente minimale de 15 minutes avant et entre les passages. Les stations ouvertes ne sont pêchées qu'à une seule reprise. Des mesures de la vitesse, à six dixièmes de la hauteur de la colonne d'eau, servent à caractériser la vitesse moyenne de celle-ci (Armour *et al.*, 1983; Léopold *et al.*, 1964) à trois ou quatre endroits sur chaque parcelle. La profondeur moyenne est également obtenue par trois ou quatre mesures sur la parcelle. Le diamètre moyen du substrat est calculé à partir des proportions estimées de blocs, galets, cailloux, gravier et sable (diamètre moyen respectif de 625, 157, 48, 18 et 2 mm). En règle générale, trois parcelles (rive gauche, centre et rive droite) sont inventoriées par segment à faciès homogène. Le choix des segments échantillonnés est aléatoire avec une probabilité inégale de sélection (Frontier, 1983), déterminée par la superficie des segments. Au total, le nombre de parcelles échantillonnées fut de 605 pour la période de 1986 à 1989 inclusivement et de 156 pour l'année 1988.

La pêche électrique est généralement pratiquée sur cette rivière de juillet à septembre. En 1988 particulièrement, elle fut réalisée du 25 juillet au 23 août. Les divers faciès d'écoulement sont visités en alternance durant la période de pêche, de façon à ne pas créer un biais systématique de la taille des juvéniles à cause de la croissance durant la saison. Finalement, il faut mentionner que l'appareil de pêche électrique utilisé convient pour des profondeurs de moins de 1,5 m. Il s'en suit que les inventaires peuvent s'effectuer sur tous les seuils et rapides, mais se dans les bassins (en moyenne 4,5 cm/s) et un maximum de 126 cm/s dans les rapides (en moyenne 34 cm/s). Les faciès échantillonnés sur la rivière de la Trinité ne sont pas tellement profonds : 33 cm en moyenne dans les seuils et 70 cm pour les zones inventoriées dans les bassins. Finalement les rapides sont caractérisés surtout par les blocs alors que les galets dominent (d'après la moyenne) les autres faciès. Il faut noter qu'en réalité ce sont les graviers et les cailloux qui dominent dans ces habitats. La représentation du substrat par un diamètre moyen crée en effet une certaine distorsion. Dans l'ensemble, il existe un recoupement assez marqué des valeurs des paramètres vitesse, profondeur et granulométrie entre les différents types d'habitat.

b) Utilisation préférentielle des habitats

À ce premier niveau, l'analyse factorielle des correspondances montre qu'il existe un lien hautement significatif entre les habitats et les groupes de taille des juvéniles ($p < 0{,}001$). On constate l'association claire entre, d'une part, les alevins et les seuils ainsi que les chenaux, et d'autre part, entre les tacons (âges 1+, 2+ et 3+) et les rapides (Fig. 3). Les zones inventoriées dans les bassins ne semblent pas être utilisées par aucune classe de longueur en particulier. Ces résultats représentent 78,8 % du lien entre les habitats et les juvéniles et constituent l'axe factoriel 1.

On peut également constater que les petits alevins sont associés surtout aux seuils alors que les individus moyens (40 à 50 mm) le sont surtout avec les chenaux (Fig. 3). Cette distinction représente 14,9 % du lien et constitue l'axe 2. Les grands alevins, quoiqu'associés aux seuils (50 à 60 mm), sont négligeables dans l'analyse, car ils ne représentent que 36 individus sur un total de 929.

c) Influence des paramètres hydromorphologiques sur l'utilisation des habitats

i) Vitesse du courant

Dans les seuils, les petits alevins sont associés aux vitesses inférieures à la moyenne alors que les plus grands le sont avec les vitesses supérieures à la moyenne (Fig. 4). La même observation peut être faite dans les chenaux, mais la tendance est moins claire. Dans les rapides, l'effet de la vitesse semble plus complexe que dans les seuils. Les vitesses inférieures à la moyenne sont associées aux individus de taille

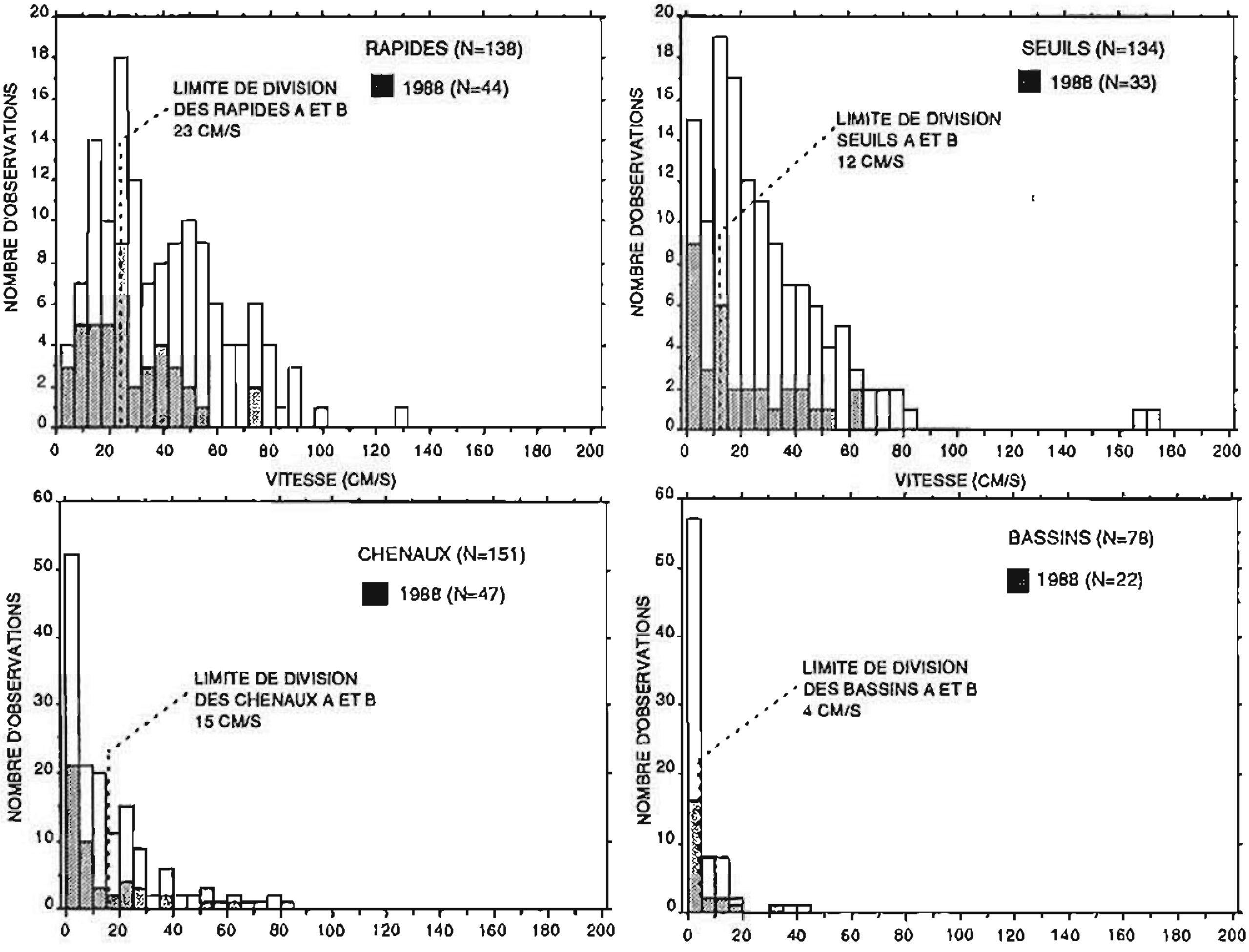


FIG. 2. (a), (b) and (c). Valeurs moyennes, minimales et maximales des paramètres hydromorphologiques mesurés à même les faciès d'écoulement échantillonnés sur la rivière de la Trinité de 1986 à 1989.

restreignent à environ 50 % des chenaux et 30 % des bassins, dans leurs parties les moins profondes.

d) Constitution de la matrice de données

Au premier niveau de l'analyse, la matrice de données est un tableau de fréquences où les colonnes représentent le nombre de juvéniles capturés à la pêche électrique dans les différents habitats (bassin, chenal, rapide et seuil) et où les lignes représentent le nombre de juvéniles dans chacune des classes de longueurs établies aux 10 mm. Au second niveau d'analyse, trois autres tableaux sont générés à partir du premier, en subdivisant les colonnes (les habitats) en fonction de la valeur moyenne des vitesses de courant, des profondeurs et des diamètres moyens du substrat observés sur les parcelles. Le premier tableau permet, au premier niveau, d'examiner l'utilisation préférentielle des habitats par les juvéniles de différentes classes de longueur. Au second niveau d'analyse, les trois tableaux suivants permettent respectivement d'étudier l'influence de la vitesse du courant, de la profondeur et de la granulométrie sur l'utilisation préférentielle des habitats par les juvéniles. L'utilisation de la longueur des juvéniles est intéressante parce qu'il existe une assez bonne correspondance entre la longueur et l'âge (Fig. 1; Caron et Bolduc, 1990).

e) Description des méthodes d'analyses

i) Analyse factorielle des correspondances

Il s'agit d'une méthode statistique multidimensionnelle qui permet d'examiner l'association entre les catégories de longueur des juvéniles et les différents types d'habitat disposés sur un tableau de fréquences. Le degré d'association entre les modalités des deux variables est jugé en considérant la proximité des catégories de longueur et des types d'habitat sur un graphique. Celui-ci est issu du tableau des fréquences, préalablement pondéré par une méthode spécifique à l'analyse des correspondances, puis soumis à une analyse factorielle, laquelle détermine les plus grands axes de variations dans les données. Ces axes factoriels, généralement les deux premiers, sont représentés sur le graphique en même temps que les catégories de longueurs et les types d'habitats. Toutefois Legendre et Legendre (1984) recommandent de ne pas baser l'analyse sur le seul examen des graphiques. Les résultats présentés ici découlent donc en partie de l'examen des graphiques et en partie de l'examen des tableaux de résultats intermédiaires (non présentés). Aucune hypothèse n'est requise concernant la normalité des données ou l'homogénéité des variances. Le calcul de la probabilité (*p*) de l'analyse se fait de la façon classique pour un Khi^2, le nombre de degré de liberté étant égal au nombre de lignes plus le nombre de colonnes moins 2. Le test du Khi^2 permet de rejeter l'hypothèse d'absence de lien entre les lignes et les colonnes, puis l'analyse décrit ce lien en détail. Des explications supplémentaires sur la méthode et les différentes étapes de calcul se retrouvent dans Escofier et Pagès (1988), Lefebvre (1983) et Benzécri *et al.* (1980).

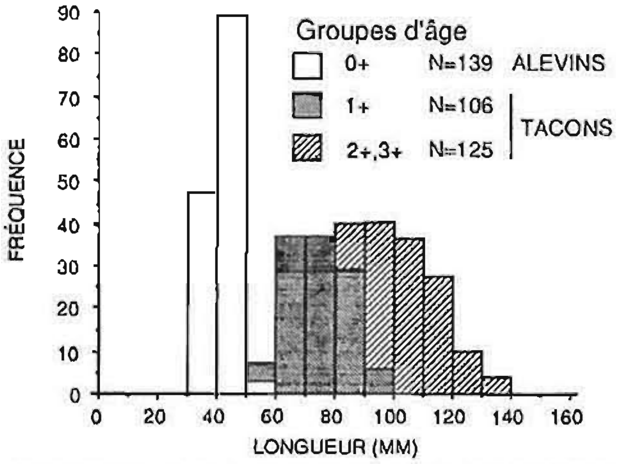


FIG. 1. Longueurs, en centimètres, atteintes par les juvéniles de différents groupes d'âge de la rivière de la Trinité de 1983 à 1989.

L'analyse factorielle des correspondances (AFC) s'est avérée particulièrement efficace pour dégager la variabilité de la matrice de données. D'abord au premier niveau, parce qu'elle a permis de vérifier s'il y avait utilisation préférentielle des habitats par les différents stades de juvéniles; puis à un second niveau, parce qu'elle permettait d'étudier l'influence des paramètres hydromorphologiques (vitesse, profondeur et granulométrie) sur cette utilisation et ce, en conservant la structure écologique mis en évidence au premier niveau de l'analyse.

ii) Analyse en composantes principales

L'AFC n'est pas adéquate pour comparer l'influence des paramètres hydromorphologiques (vitesse, profondeur et granulométrie) entre les années. Cette comparaison a donc été réalisée par une analyse en composantes principales appliquée aux paramètres hydromorphologiques observés pour chaque année. Les vitesses de courant, les profondeurs et les diamètres moyens du substrat observés sur les parcelles ont été attribués à chaque poisson capturé de façon à créer une matrice de données individus X descripteurs. L'analyse a été effectuée en mode R, ce qui implique d'abord le calcul d'une matrice d'association entre les descripteurs (Legendre et Legendre, 1984).

Résultats

a) Caractérisation du faciès d'écoulement de la rivière de la Trinité

Les figures 2a, 2b et 2c illustrent quelques caractéristiques des faciès d'écoulement échantillonnés sur la rivière de la Trinité de 1986 à 1989. Il s'en dégage que le registre de vitesse du courant est relativement peu étendu, avec un minimum de 0 cm/s

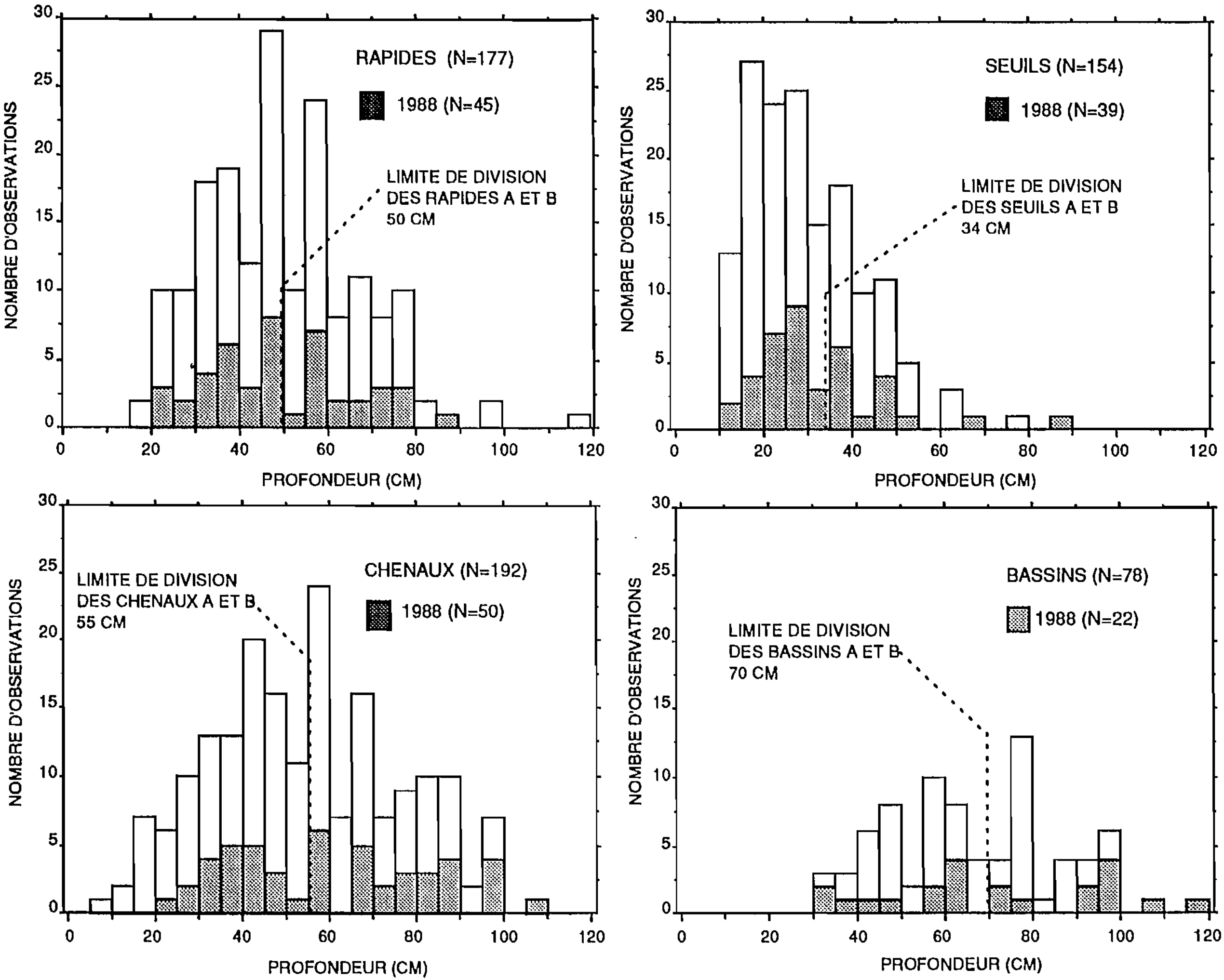


FIG. 2. (b)

intermédiaire du groupe d'âge 1+ (70–80 mm), alors que les vitesses les plus élevées le sont avec les tacons 1+ de 60 à 70 mm. La même ségrégation s'observe chez les tacons d'âge 2+ et 3+; les faibles vitesses sont associées au groupe de taille intermédiaire (100–110 mm) alors que les vitesses élevées le sont avec les petites et les grandes tailles (90–100 mm et 110–120 mm) du groupe d'âge. L'effet de la vitesse sur l'utilisation des rapides par les tacons est plus faible que celui qu'exerce le même paramètre dans les seuils et les chenaux sur les alevins. Dans les chenaux, les vitesses faibles sont associées aux alevins de 40 à 50 mm. L'augmentation de vitesse se traduit par une réduction de l'abondance des alevins mais pas de celle des tacons.

ii) Profondeur

Dans les seuils, il y a une relation positive entre la profondeur et la taille des alevins (Fig. 5). Or, il y avait également une relation positive entre la vitesse et la taille des alevins. Donc les seuils de profondeur et de vitesse faibles sont occupés par les petits alevins, alors que les seuils de profondeur et de vitesse plus élevés le sont par les plus grands. Dans les chenaux, les faibles profondeurs sont associées aux alevins de taille moyenne (40 à 50 mm). L'augmentation de la profondeur diminue l'association avec les alevins sans toutefois accroître celle avec les tacons. Dans les rapides, les faibles profondeurs sont associées avec les individus de taille intermédiaire du groupe d'âge 1+ (70–80 mm) alors que les profondeurs plus élevées le sont avec ceux de plus grande taille (80–90 mm). Le même patron d'utilisation s'observe chez les groupes d'âges 2+ et 3+. La relation entre la vitesse et la profondeur est inverse dans les rapides, contrairement aux seuils et aux chenaux où elle était directe. Dans les bassins, il existe une relation directe très marginale entre la profondeur et la taille des juvéniles.

iii) Granulométrie

Les effets les plus marqués du changement de la granulométrie (Fig. 6) se font sentir dans les chenaux (sur l'axe 2) et les rapides (sur l'axe 1). Dans les chenaux, l'augmentation de la granulométrie moyenne se traduit par une diminution de la présence des alevins et une légère augmentation de celle des tacons. Dans les rapides, l'augmentation de la granulométrie se traduit par une présence accrue des tacons de grande taille. On observe peu d'effets du changement de la granulométrie dans les seuils et les bassins.

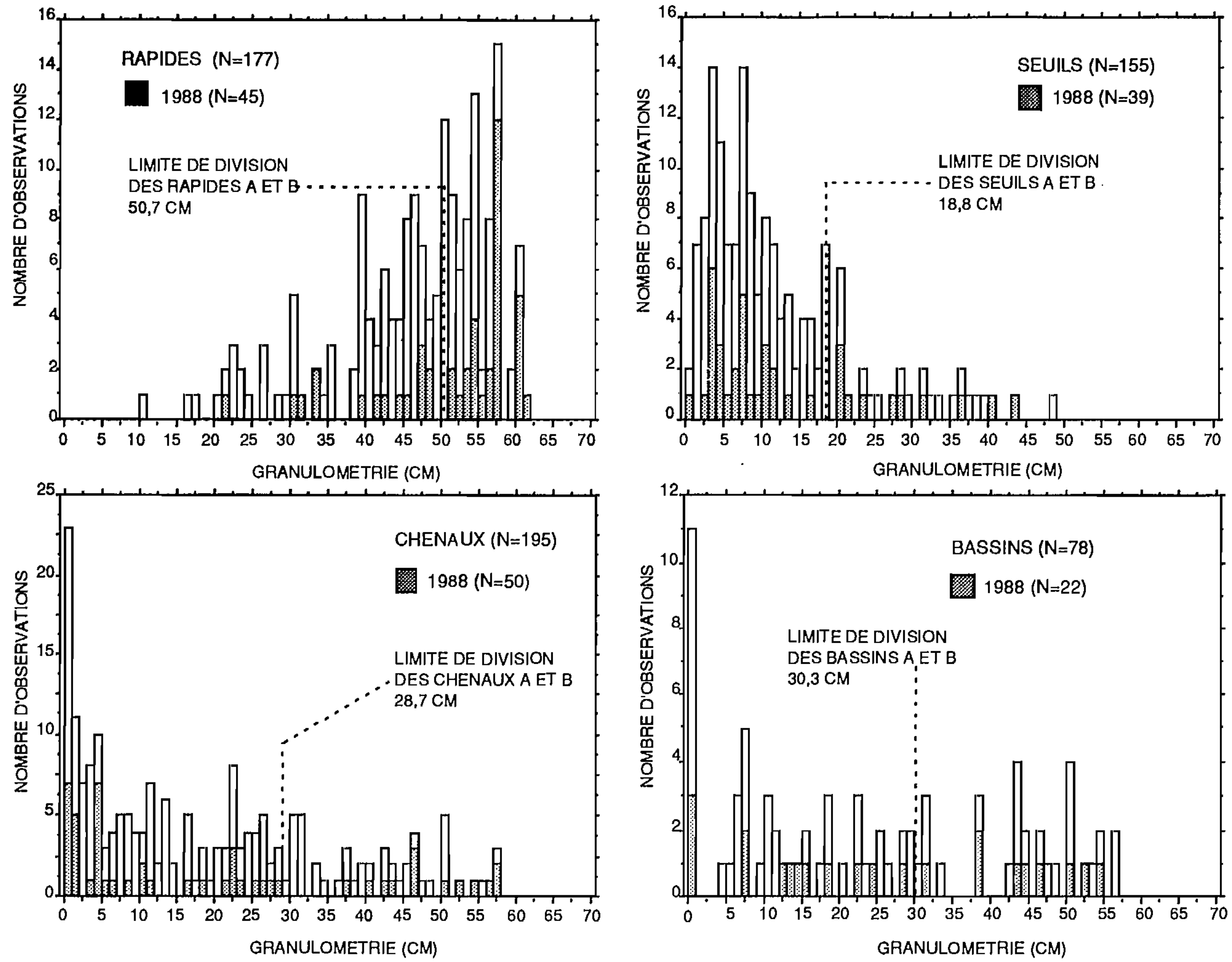


FIG. 2. (c)

d) Résultats de l'analyse en composantes principales

Le tableau 1 résume les résultats de l'A.C.P. appliquée aux vitesses, aux profondeurs et aux diamètres moyens du substrat attribués aux juvéniles capturés sur les parcelles pêchées de 1986 à 1989. La valeur relative des paramètres hydromorphologiques comme descripteurs de l'habitat change d'une année à l'autre. Cependant, les trois paramètres expliquent ensemble environ 40 % des observations et la proportion demeure assez constante d'une année à l'autre.

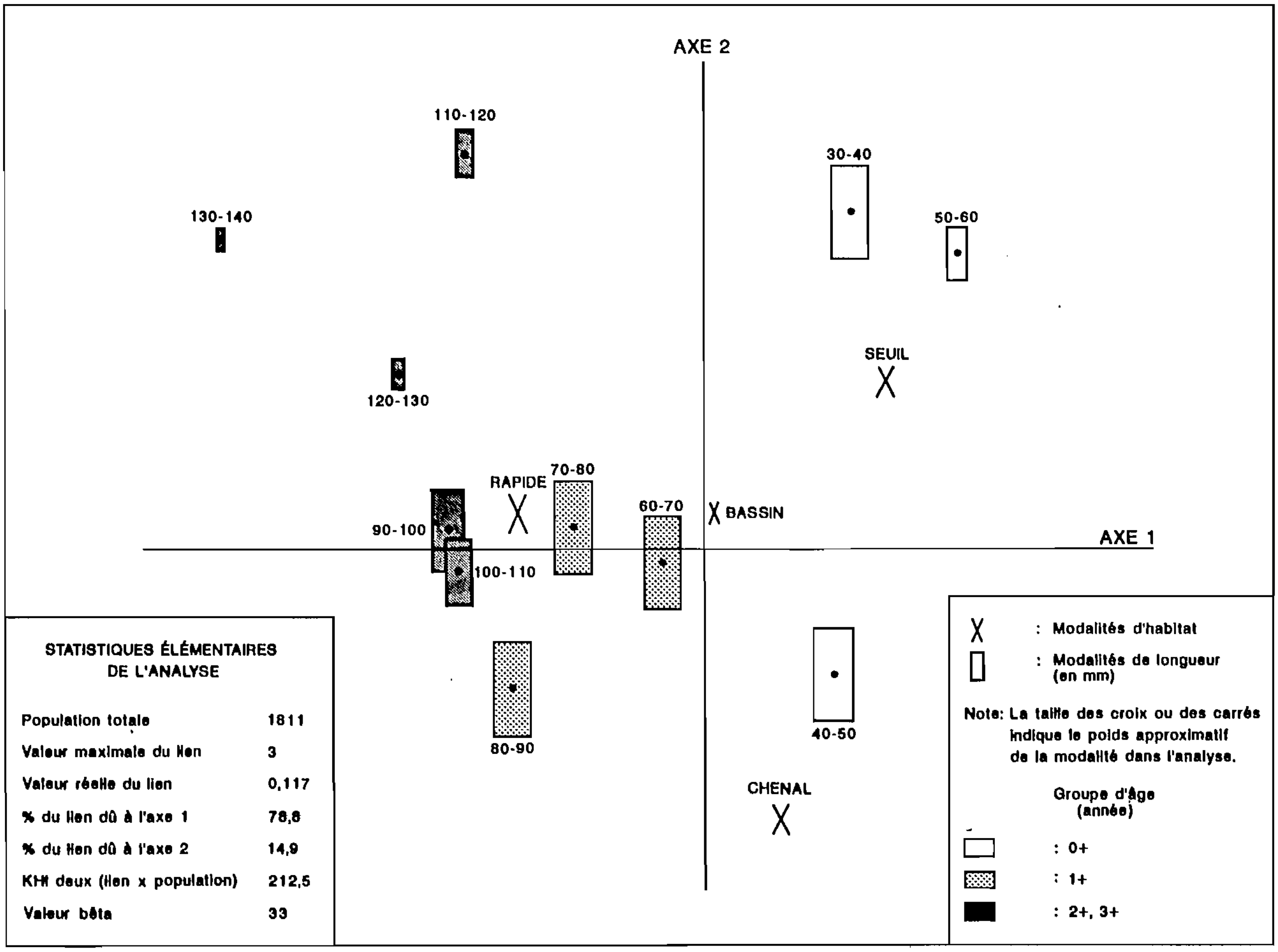
Discussion

a) Utilisation préférentielle de l'habitat

Le premier niveau d'analyse montre clairement qu'il existe une utilisation préférentielle des seuils par les petits alevins (30–40 mm) et des chenaux par des alevins de plus grande taille (40–50 mm), alors que les tacons de tout âge utilisent surtout les rapides. Les zones inventoriées dans les bassins ne semblent pas faire l'objet d'une utilisation préférentielle par aucun groupe de juvéniles. Les associations seuils-alevins et rapides-tacons semblent faire l'objet d'un consensus dans la littérature où l'on a défini les différents types de faciès d'écoulement (Jones 1975; Symons et Héland 1978; Belzile *et al.* 1982; Boudreault 1984; Caron 1987; Côté *et al.* 1987a). Toutefois, l'association entre les chenaux et les alevins de plus grande taille constitue, semble-t-il, un nouvel élément d'information.

Le fait que les alevins sur les seuils soient plus petits que ceux qui utilisent les chenaux laisse croire que ce dernier habitat leur est plus favorable. Cette situation pourrait être le reflet d'une moins grande compétition à ces endroits puisque les densités que l'on y trouve sont beaucoup plus faibles (Caron et Talbot, 1992). On sait, en effet, que la compétition intraspécifique résultant de la densité peut influencer la croissance (Gibson et Dickson, 1984; Kennedy et Strange, 1986). Par ailleurs, il est également possible qu'il s'agisse d'un déplacement autonome des plus grands alevins vers les chenaux.

Des analyses identiques réalisées sur les données des autres années (résultats non présentés) montrent que l'utilisation préférentielle des habitats se répète d'une année à l'autre. Il semble donc que les juvéniles de différents âges (et, par conséquent, de taille), bien que capables d'utiliser différents habitats, montrent une



STATISTIQUES ÉLÉMENTAIRES DE L'ANALYSE

Population totale	1811
Valeur maximale du lien	3
Valeur réelle du lien	0,117
% du lien dû à l'axe 1	78,6
% du lien dû à l'axe 2	14,9
KHI deux (lien x population)	212,5
Valeur bêta	33

FIG. 3. AFC et projection sur les deux premiers axes factoriels des faciès d'écoulement et des modalités de longueurs des juvéniles capturés par pêche électrique sur la rivière de la Trinité en 1988.

TABLEAU 1. Pourcentage de la présence des juvéniles, dans les divers faciès d'écoulement, expliqué par les variables vitesse, profondeur et granulométrie d'après les analyses en composantes principales exécutées sur les données de la rivière de la Trinité pour les années 1986 à 1989.

Année	Nombre de juvéniles	Vitesse	Profondeur	Granulométrie	Variation totale expliquée (%)
1986	2 269	31,0	5,0	5,5	41,5
1987	1 166	10,6	5,3	22,7	38,6
1988	1 811	8,7	23,8	5,5	38,0
1989	2 443	10,1	26,8	2,6	39,5

préférence pour certains d'entre eux. Ils effectueraient donc des déplacements d'un habitat à l'autre à l'intérieur d'une rivière à la recherche d'habitat qui conviennent mieux à leur taille. Ce premier niveau d'analyse suggère qu'il soit possible d'améliorer les évaluations de potentiels salmonicoles (réalisées notamment par la photo-interprétation) en tenant compte de la disponibilité et/ou de l'agencement des différents types d'habitat en rivière.

b) Influences des paramètres hydromorphologiques sur l'utilisation de l'habitat

Le second niveau d'analyse montre que les paramètres vitesse du courant, profondeur et granulométrie, mesurés à l'échelle des parcelles échantillonnées, ne modifient pas l'utilisation préférentielle de l'habitat par les juvéniles, mais que les différentes valeurs de ces paramètres sont associées à des juvéniles de tailles différentes. De plus, la relation entre ces paramètres hydromorphologiques semble différente selon les types d'habitat, de même que l'influence qu'ils exercent sur les juvéniles de différentes tailles.

La comparaison de ces observations avec celles de la littérature doit être faite avec précaution parce que les définitions des types d'habitat ainsi que les méthodes d'échantillonnage et de traitement sont parfois très différentes. Toutefois, certains rapprochements peuvent être faits, particulièrement en ce qui concerne les seuils. Ainsi Symons et Heland (1978), travaillant sur des seuils artificiels en laboratoire, ont montré que la vitesse et la profondeur choisies par les juvéniles augmentaient avec la taille de ceux-ci, tout comme dans notre étude. Dans un même ordre d'idées et bien qu'ils ne traitent pas exclusivement des alevins sur les seuils, Rimmer *et al.* (1984) et Morantz *et al.* (1987), rapportent que la vitesse du courant choisie par les juvéniles est fonction de la taille, alors que Kennedy et Strange (1982) font la même constatation, mais cette fois, en fonction de la profondeur. Pour leur part, De Graaf et Bain (1986) concluent que le substrat n'est pas important dans les seuils, une constatation identique aux observations réalisées dans cette étude.

Dans les rapides, la vitesse et la profondeur sont inversement reliées. Toutefois, le lien entre la taille des tacons et ces paramètres n'est pas monotonique comme il l'était pour les alevins et ces mêmes variables sur les seuils. Par exemple, les rapides à vitesse faible sont associés à des tacons de taille intermédiaire (70–80 et 80–90 mm) alors que ceux à vitesse élevée sont associés à des petits (60–70 mm) et à des grands tacons (90–100 et 110–120 mm). La relation entre la taille des tacons et la profondeur présente le même genre de complexité. L'influence de la granulométrie semble plus claire, une augmentation du diamètre moyen se traduisant par une augmentation de la taille des tacons. Ils faut souligner que les rapides sont des segments très hétérogènes où l'on retrouve, à l'intérieur même d'une parcelle, de nombreux micro-habitats. Il s'en suit que l'association entre les juvéniles et les caractéristiques de la parcelle sont complexes. La compréhension claire de ces associations nécessitera vraisemblablement des recherches spécifiques.

Dans les chenaux, le passage des basses vitesses vers les plus hautes, de même que des faibles profondeurs vers les plus grandes, s'accompagne d'une diminution de la présence des alevins, sans qu'il y ait modification de celle des tacons. L'augmentation de la granulométrie dans les chenaux est associée à une diminution de la présence des alevins alors qu'une légère tendance à l'augmentation de la présence des tacons se dessine.

Il apparaît que, dans la rivière de la Trinité, l'étendue de la valeur des paramètres hydromorphologiques soit relativement faible et se recoupe beaucoup entre les faciès. Ces paramètres ne peuvent donc pas avoir une influence marquée sur l'utilisation de l'habitat par les juvéniles. Il est probable que d'autres facteurs interviennent: les habitats eux-mêmes, représentant l'interaction entre les paramètres hydromorphologiques, la pente du lit de la rivière, ainsi que d'autres éléments comme la séquence d'apparition des faciès, la productivité, la compétition inter et intraspécifique, la prédation, la température, etc.

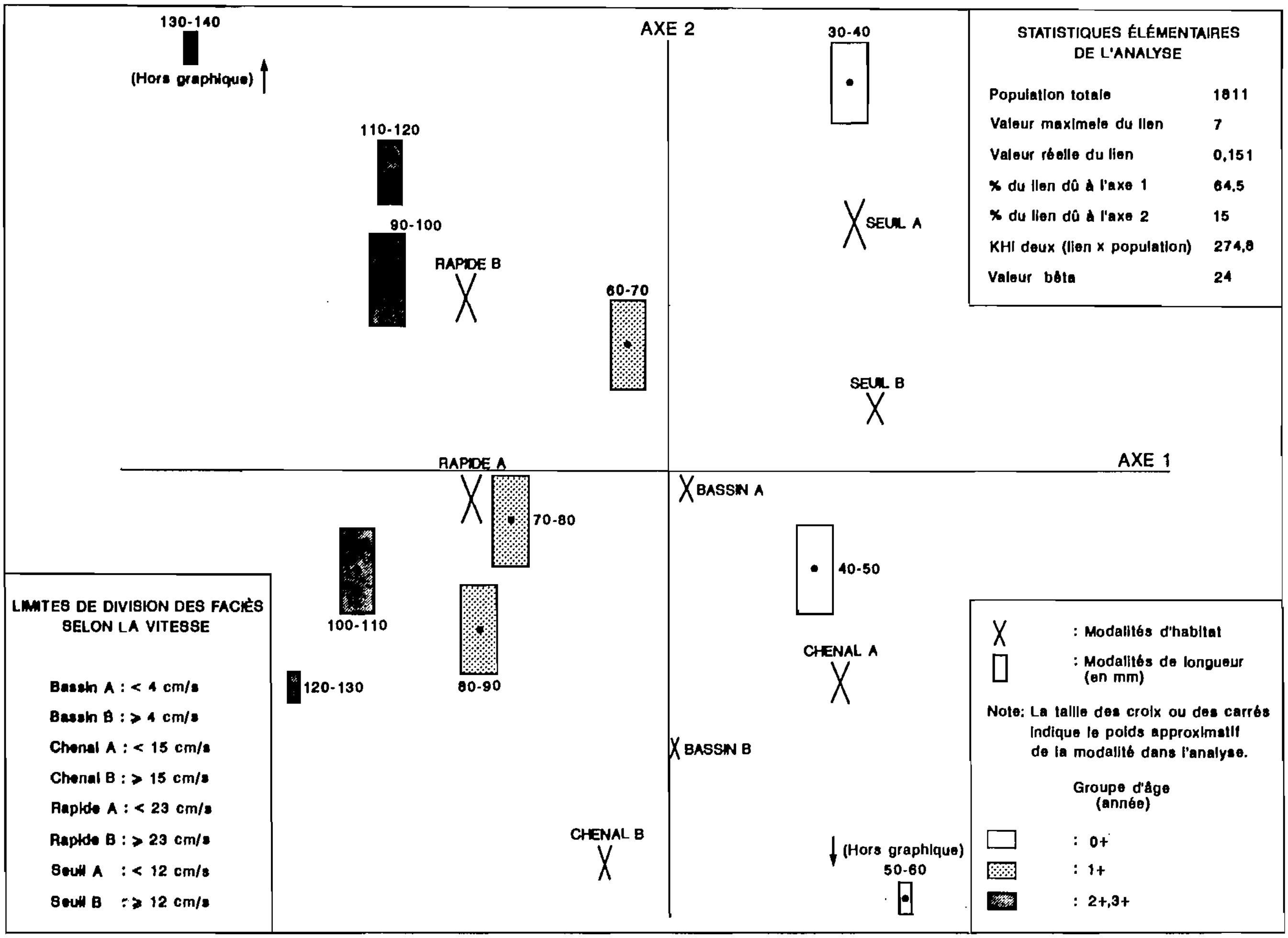


FIG. 4. AFC et projection sur les deux premiers axes factoriels des faciès d'écoulement, séparés en basses et hautes vitesses, et des modalités de longueurs des juvéniles capturés par pêche électrique sur la rivière de la Trinité en 1988.

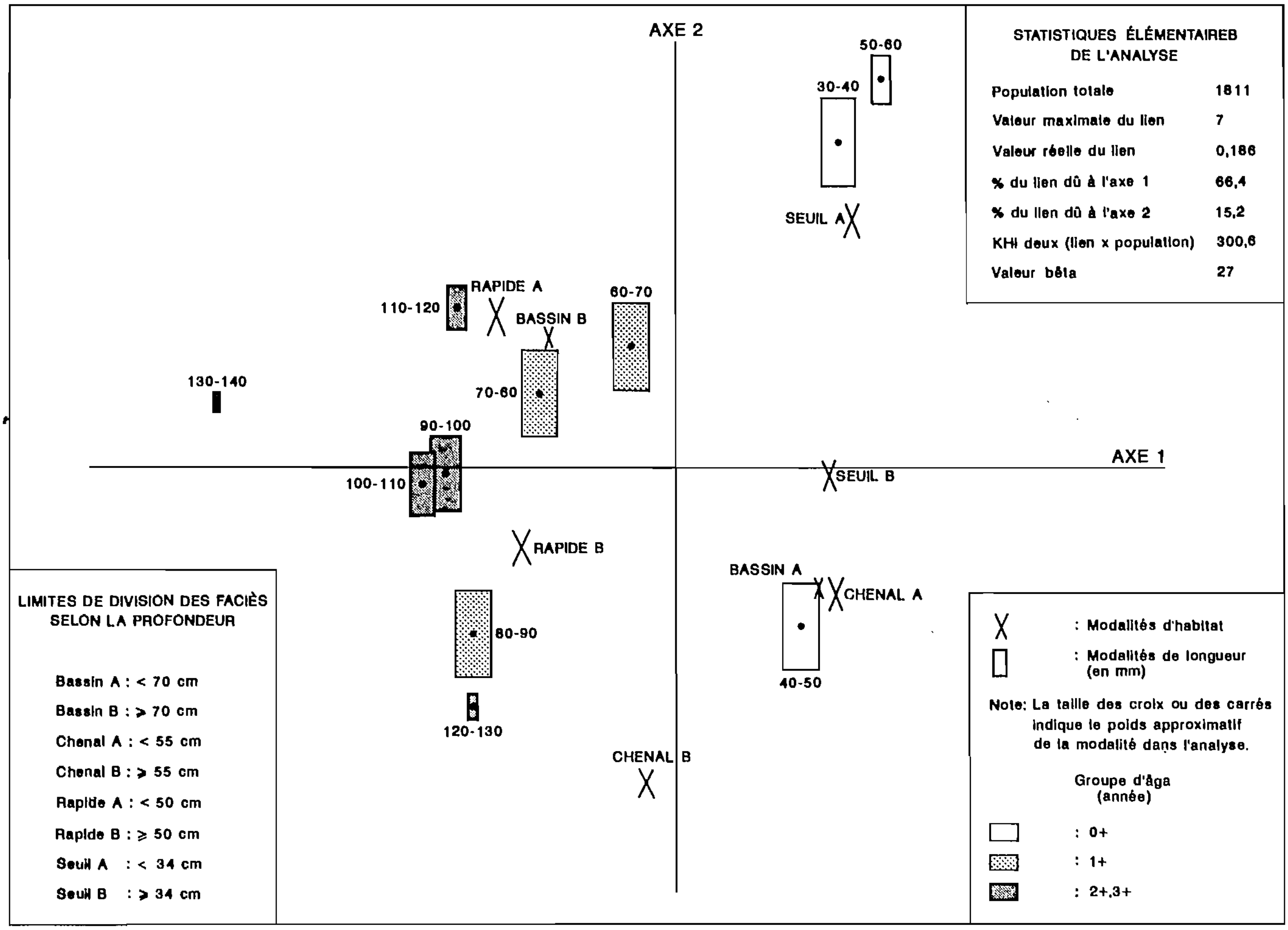
c) Comparaison interannuelle de l'influence des paramètres vitesse, profondeur et granulométrie

Cette analyse a montré que la proportion relative de la variabilité expliquée par chaque variable change d'une année à l'autre. La variabilité expliquée par les trois variables simultanément reste à peu près constante d'une année à l'autre, soit environ 40 %, ce qui est relativement faible. Ces résultats se comparent avec ceux de Heggenes et Saltweit (1990), particulièrement dans le fait que la vitesse du courant, à elle seule, explique moins de 35 % de la variance (31 % maximum dans notre étude). Il est donc possible que la force du lien entre les juvéniles et les paramètres hydromorphologiques (par exemple la taille des alevins et la vitesse sur les seuils) change d'une année à l'autre.

Au terme du second niveau d'analyse, il apparaît plus difficile d'améliorer les évaluations des potentiels salmonicoles à partir des conditions hydromorphologiques que ce ne l'était à partir de l'utilisation préférentielle des habitats. Les relations entre les variables mésologiques et entre celles-ci et les juvéniles apparaissent différentes entre les habitats et plus ou moins marquée entre les années. Seules les relations établies sur les seuils sont claires. Les influences exercées par les paramètres hydromorphologiques sur les juvéniles dans les autres habitats, nécessiteront d'être analysées plus spécifiquement. Il semble toutefois, que ces influences soient en relation avec la taille des juvéniles à l'intérieur et entre les groupes d'âge.

Conclusion

Il existe une utilisation préférentielle des habitats par les différents stades de juvéniles. Cette conclusion, tirée de l'analyse des données, constituait déjà un élément connu dans la littérature. Il apparaît ainsi que l'évaluation des potentiels salmonicoles pourrait être améliorée en tenant compte de cet élément. Il pourrait être intégré en considérant l'agencement et/ou la disponibilité des différents habitats sur une rivière. Par ailleurs, les paramètres hydromorphologiques ne modifient pas sensiblement cette utilisation préférentielle, du moins pas dans une rivière du gabarit de la Trinité, mais leurs différentes valeurs sont associées avec des juvéniles de taille différente dans les divers habitats. Parce que la vitesse et la profondeur sont faibles dans une rivière de cette taille, la granulométrie n'exerce pas une influence marquée et celle-ci n'est pas partout la même. La situation est



STATISTIQUES ÉLÉMENTAIRES DE L'ANALYSE

Population totale	1811
Valeur maximale du lien	7
Valeur réelle du lien	0,186
% du lien dû à l'axe 1	66,4
% du lien dû à l'axe 2	15,2
KHI deux (lien x population)	300,6
Valeur bêta	27

FIG. 5. AFC et projection sur les deux premiers axes factoriels des faciès d'écoulement, séparés en profondeurs faibles et grandes, et des modalités de longueurs des juvéniles capturés par pêche électrique sur la rivière de la Trinité en 1988.

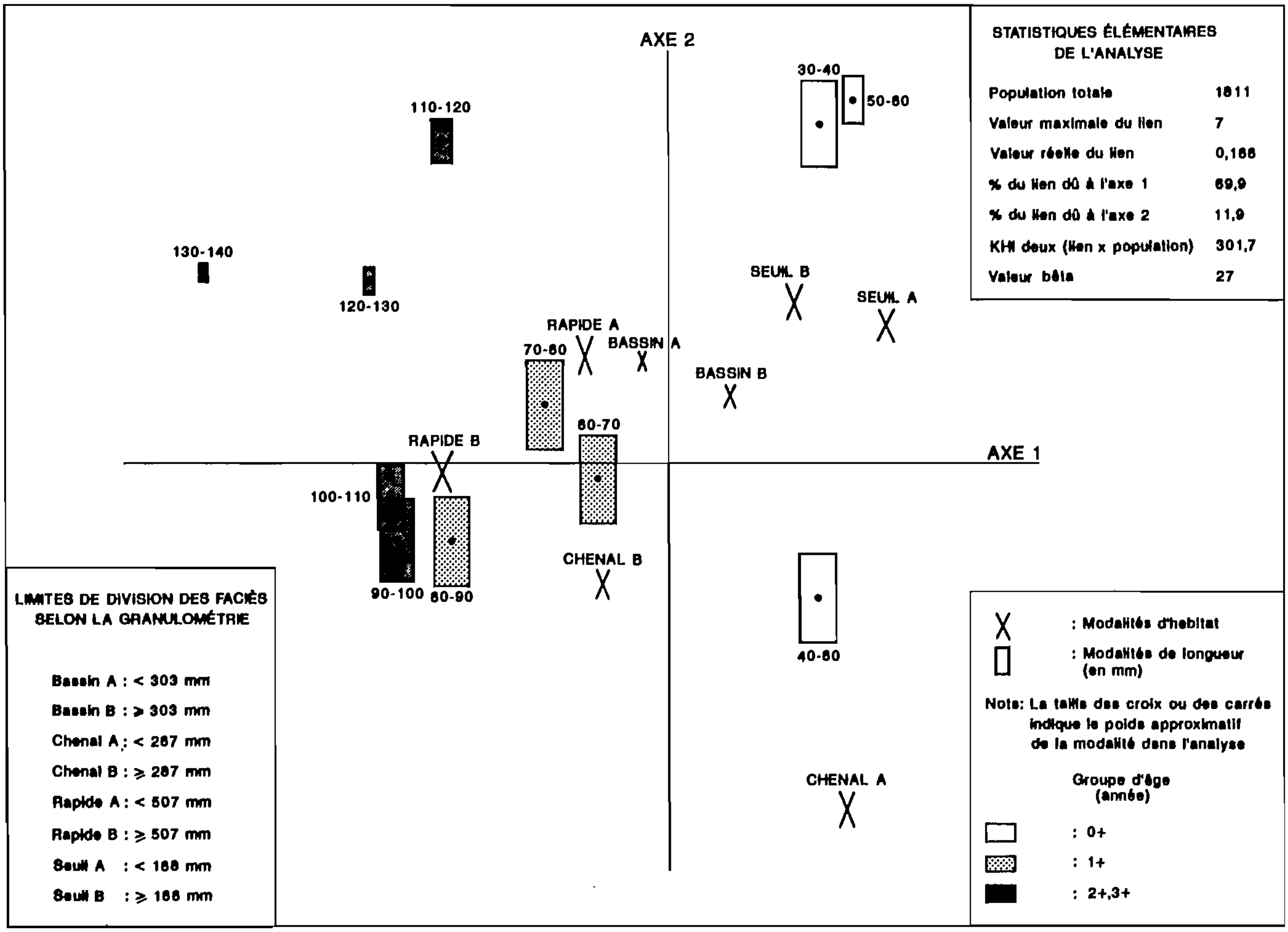


FIG. 6. AFC et projection sur les deux premiers axes factoriels des faciès d'écoulement, séparés en granulométrie fine et grossière, et des modalités de longueurs des juvéniles capturés par pêche électrique sur la rivière de la Trinité en 1988.

probablement différente dans une grande rivière où en vertu des vitesses et des profondeurs plus grandes, des habitats sont créés à l'aval des blocs, ceux-ci agissant alors comme des déflecteurs (home-rock).

Sur un plan méthodologique, il pourrait être difficile de procéder avec des méthodes paramétriques à une analyse statistique équivalente à celle proposée dans cet article, à moins de procéder à une analyse séparée pour chaque type d'habitat. En effet, non seulement il faut tenir compte de plusieurs variables de types différents, mais il faut aussi tenir compte de la structure écologique entre les variables, lesquelles ne sont pas nécessairement liées linéairement. Dans l'analyse factorielle des correspondances, les faciès d'écoulement, représentant l'action combinée de plusieurs facteurs, interviennent en structurant l'information recueillie sur les parcelles pêchées à l'électricité, et mettent en évidence la nature exacte du lien entre les paramètres hydromorphologiques et la population de juvéniles.

Remerciements

Cette étude a été rendue possible grâce à la collaboration entre les trois organisations impliquées. Hydro-Québec a octroyé les fonds nécessaires pour mener l'analyse, alors que le ministère du Loisir, de la Chasse et de la Pêche du Québec a bien voulu nous donner accès à l'importante banque de données colligée depuis plusieurs années sur la rivière de la Trinité. L'analyse des données a été réalisée par le Groupe Environnement Shooner inc.

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Re-Evaluation of Habitat Classification Criteria for Juvenile Salmon

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Juvenile Atlantic salmon (*Salmo salar*) habitat classification is a useful tool for management where knowledge of egg deposition rates are required for stream enhancement, or to determine the productive capacity of a river system. A habitat classification system has been developed and is currently in use in Québec since the mid-1980's. This method has been re-evaluated with data from an experimental river program, and a new simpler method is suggested. In particular, only 2 categories of habitat are retained, and only information on stream type (rapids, runs, flats or pools) and presence of sand is required. The new method proved to be quite effective in discriminating between densely and sparsely populated areas.

La classification des habitats du saumon atlantique (*Salmo salar*) juvénile est un instrument utile de gestion lorsqu'on a besoin de calculer le nombre d'œufs requis pour la mise en valeur d'un cours d'eau, ou pour déterminer la capacité de production d'un réseau hydrographique. Un système de classification des habitats a été mis au point et est actuellement utilisé au Québec depuis le milieu des années 80. La méthode a été réévaluée à l'aide de données provenant d'un programme de recherche sur des rivières expérimentales et on propose une nouvelle méthode plus simple. On retient en particulier deux catégories seulement d'habitat, et la seule information nécessaire concerne facies d'ecoulement (rapide, seuil, cheval ou bassin) et la présence de sable. La nouvelle méthode s'est révélée très efficace pour distinguer entre les zones densément et faiblement peuplées.

Introduction

Estimation of usable juvenile Atlantic salmon (*Salmo salar*) habitat in streams and rivers is required for the estimation of stocking densities (egg deposition) for particular streams and as a predictive tool for estimating smolt production. Habitat mapping from aerial photographs has been used to evaluate several salmon rivers in Québec (Dubois et Clavet 1977, Boudreault 1984). A method for converting the habitat characteristics into a theoretical value for salmonid production potential was presented by Coté (1987) and Coté et al. (1987) and accepted as the normalized method in Québec.

The classical classification scheme, based on salmon habitat preferences derived from the practical experience of salmon experts, combines coded information from substrate composition and stream attributes (rapids, runs, flats, meanders, pools). The coded scores given were 0, 1, or 2 (from poor to excellent respectively) for each of particular substrate composition and stream attributes. Multiplication of the assigned scores for each substrate composition and stream type rendered habitat production values of 0, 1, 2 or 4. Stream segments with values of 0 were classified as type III, or unproductive habitat (assumed to produce no salmon). Segments of value 1 or 2 were classified as type II, or average habitats. Segments with scores of 4 were classified as type I, or ideal habitats.

Symons and Heland (1978), Symons (1979), Elson (1957, 1975) and others have derived optimal densities of Atlantic salmon in suitable habitat in order to maximize productivity. Based on estimates of survival and territoriality, and using empirical and statistical methods, Symons (1979) was able to provide smolt production estimates for salmon rivers. Elson (1975), using a stock-recruitment function, arrived at a suggested stocking density of 240 eggs 100 m^{-2}. However, what all these proposed methods have in common is that "suitable" habitats must be available, without being able to rigorously define actual physical characteristics of these habitats. Furthermore, it is unclear to us whether only "suitable" habitats need to be considered, whether "suitable" habitats may actually vary in quality, or to what extent habitat use by juvenile salmon is influenced by external factors and represents a very dynamic process. Symons (1971) demonstrated that population density responded in a predictable manner to food availability. Gibson and Dickson (1984) related growth rate and competition in natural conditions, and Gibson (pers. comm.) found that juvenile salmon could be found in large numbers in various and quite different environments. There is a need to define which habitats can hold juvenile salmon and which cannot, and to be able to estimate the quality of each type of habitat from field surveys.

From experimental programs and modelling exercises, as well as from an apparent lack of a relationship between smolt production and juvenile densities in habitat types I and II, the assumptions of the classification scheme, and particularly the assumption of non-negligible contribution from habitats of type III, have been questioned (Caron 1990).

This paper presents an alternate classification system based on experimental data from three Québec rivers in different geographical areas, and discusses the implications of general application of any classification method derived for salmon production.

Methods

An experimental program started in 1983 was used to validate the habitat classification system of Coté et al. (1987). The database for the present work is derived from the following rivers: the Trinité River on Québec's North-Shore, the St-Jean River on the Gaspé peninsula, and the Bec-Scie River on the island of Anticosti. The 3 geographical areas from which the rivers were selected are very different, ranging from the bedrock of the Laurentian shields to sandy loam of glacial and fluvial deposits of the St-Lawrence river valley. The mouths of the 3 rivers are all within 1°of latitude of each other, and within a 225 km radius (Fig. 1).

Although these rivers are very different geomorphologically and hydrologically, they have healthy populations of Atlantic salmon, a requirement for the determination of habitat use. Caron and Bolduc (1991) concluded, by demonstrating that the life cycles of salmon are unique in each river, that the stocks required individual management approaches.

Habitat classification was achieved by aerial photographs of the Trinité River (Clavet 1982) and Saint-Jean River (Boudreault 1988), and from direct measurements in the field for the Bec-Scie River (Caron and Fournier 1989) according to the method proposed by Coté et al. (1987). The river is divided into homogeneous segments with respect to stream type (rapids, runs, flats, pools, etc.) and substrate composition.

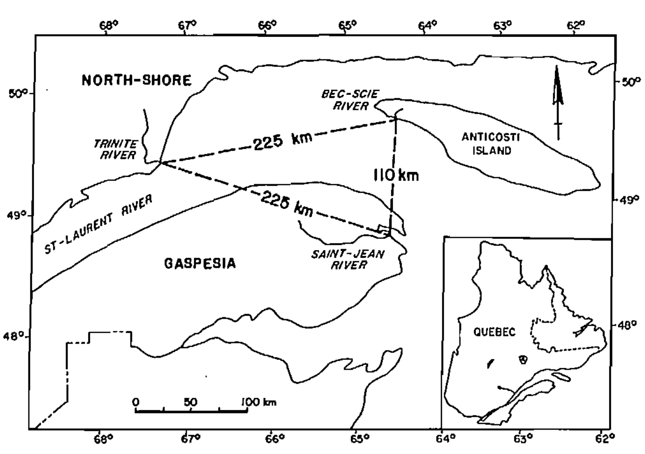

FIG. 1. The Saint-Lawrence estuary showing the location of the three experimental rivers used in this paper. Inset: The province of Québec.

On the Trinité and Bec-Scie rivers, the river bed was divided according to homogenous segments along the entire drainage system. These segments ranged in area from 200 m^2 (for falls) to 618,000 m^2 (for a reservoir), but the majority range in size from 1,000–25,000 m^2. Each experimental segment was selected randomly without replacements among all available segments, taking into consideration the size of each segment (simple random weighted selection without returns, also called selection with proportional probabilities (Frontier 1983)). Samples stations of 100 m^2 were selected at random within each segment in parts of the rivers less than 1.5 m depth. On the St-Jean River, the original experimental stations were determined according to accessibility to the sites and dispersion along the river drainage system. In all cases, the exact sampling stations are replicated yearly.

Sampling takes place in August using a classical depletion sampling method (Caron and Ouellet 1987). The sampling stations retained for this analysis are closed. This is done by extending a net around the perimeter of the station in order to prevent immigration or emigration during sampling. The operator of the electro-fishing apparatus is flanked by one or two assistants who collect the narcotized specimens. All fish are collected, measured then placed in a holding tank outside the station. A sample of fish are kept for detailed analysis (weight, length, age and sex). A minimum of three passes (sweeps) are done 30 min. apart. Population estimates are obtained by the Zippin population estimation method (Zippin 1958).

At each station, water temperature, water velocity and mean depth are recorded. Substrate composition is determined for each station by the sampling team. We used electro-fishing apparatus of model Coffelt BP-1C on the Trinité River, Dirigo 700 on the Saint-Jean and Marine Electric model Safari 300 on the Bec-Scie River.

In this paper, we chose to analyze total juvenile density even though the actual habitat preferences might differ between fry and parr in order to remain within the objectives of the present research. Our purpose is to discriminate between good and poor salmon habitat rather than to develop a classification system that will corroborate some predicted or predictable densities. The exercise is thus to produce a qualitative rather than a quantitative classification system. In this paper, we consider good salmon habitats to be those that hold approximately 20 juvenile salmon of any age or size, ie. habitats that are used by salmon.

Results

The correlation between fry and parr densities varies greatly among rivers, being 0.06 (n=81) for Trinité to 0.66 (n=35) for Bec-Scie and -0.15 (n=36) for St-Jean. Despite this apparent lack of overall association (at each individual station), the trends in stream type and bed type use were similar, with both age-groups found at high densities in rapids and runs and at lower, although more variable, densities in flats, meanders and pools (Table 1).

Verification of the Traditional Classification Method

The traditional classification method derived by Coté et al. (1987) gives variable results. Figure 2 shows the mean overall densities (total of parr and fry, with distribution) for each class and each river as determined from data on biological and physical characteristics collected at each specific station. If station data are used (data on substrate composition and stream type from the particular station, as opposed to the data derived from aerial photographs of river segments), it appears that the classification method of Coté (1987) describes suitable habitat for the Trinité and Bec-Scie Rivers. However, there seems to be relatively little qualitative difference between type I and II habitats, both appearing to be good rearing areas, whereas type III habitats have substantially reduced densities. Because the types of habitats sampled are limited by existing field conditions, only 3 stations were classified as type III in the entire data set, making any conclusions regarding the variance and validity of these observations subject to verification.

The relationship between point population estimates (represented by a 100 m^{-2} station) and river segments categories, as classified from aerial photographs according to the method of Boudreault (1984) and Coté et al. (1987), is poor (Fig. 3). In this case, the number of error terms increases. We are faced with the difficulty of describing a large area (often more than 10,000 m^{-2}) with a "point" estimate of biological and physical characteristics, in addition to the inherent error levels at specific stations. The averages do not differ systematically between categories for the Trinité but seem to follow the overall expected trend of decreasing densities for the Bec-Scie River. The better fit with the Bec-Scie River may be due to the on-site evaluation of segment substrate composition, as opposed to the estimation from aerial photographs for the other rivers (see Methods). The variances are highly heterogeneous among habitat classification, but these differences are not significant when the estimates are natural-log transformed (Chi-squared=12.2, df=6, P=0.057). Moving from what is considered average to unproductive salmon habitat has little effect on the mean but has a positive effect on the variance, indicating that some habitat types are more predictable than others, or that in reality it incorporates productive habitats along with unproductive habitats.

The efficiency of a classification method can be tested with discriminant analysis. Since the method by Coté et al. (1987) was designed to separate habitat with variable density of juvenile salmon irrespective of their size, we use parr and fry abundance as 2 separate dependent variables, and the classification method as the independent variable. In the Trinité River, 53.8% of stations were misclassified by discriminant analysis (Table 2), but this proportion is only 11.1% for the

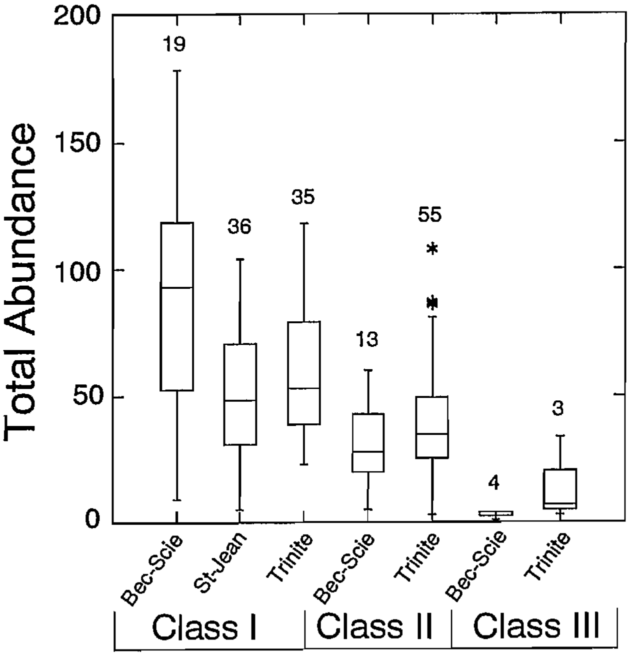

FIG. 2. Box plot representing the total juvenile salmon abundance (per 100 m^2) for each category of Coté et al. (1987)'s salmon habitat classification system. In this case, the categories were determined for the station sampled. The horizontal line in the box is the median, the upper and lower ends of the box are the 75- and 25% quartiles, the vertical lines are the ranges and the asterisk are outliers. See Wilkinson (1986) for more information on box and whisker plots. The number above the box is the sample size (n). A decrease in density from class I to III is evident, but class I and II overlap to a greater extent.

TABLE 1. Average densities (per 100 m^2) of salmon fry and parr by stream type and for all rivers in the present study.

Stream type	St-Jean		Bec-Scie		Trinité		Mean	
	parr	fry	parr	fry	parr	fry	parr	fry
Rapids	52.75	15.08	—	—	23.73	17.58	38.24	16.33
Runs	23.71	17.75	40.75	45.60	18.48	49.04	27.65	37.46
Flats	—	—	12.83	8.00	17.38	26.67	15.11	17.34
Meander	—	—	22.71	7.14	—	—	22.71	7.14
Pools	—	—	22.00	4.50	8.38	15.56	15.19	10.03
Mean	33.39	16.86	31.26	29.11	17.71	27.99		

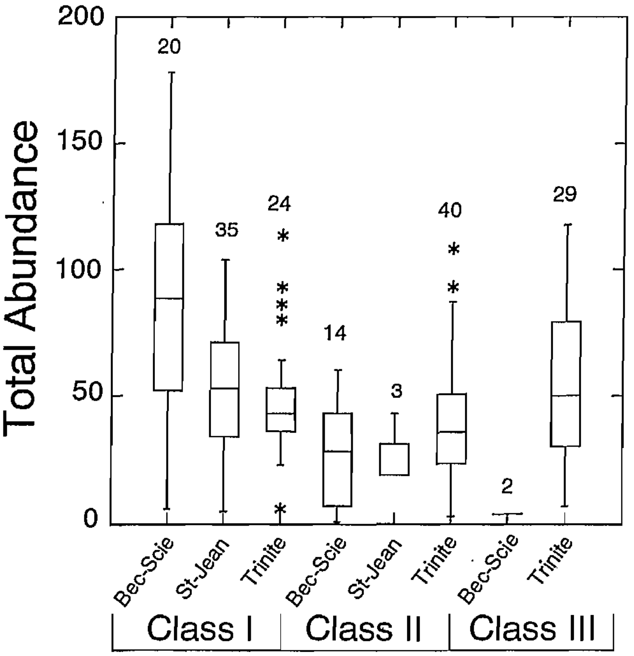

FIG.3. Box plot of total juvenile abundance with the habitat classification system derived from aerial photographs of river segments. The habitat categories are for the segment that contained the stations sampled. The box plot is as in Fig. 2. The differences between the three classes is much less evident than in Fig. 2, perhaps due to the low resolution of aerial recognition, or to the averaging effect of the method for large areas.

TABLE 2. Discriminant analysis results for the habitat classification method described by Coté (1987) and Coté et al. (1986). Results shown are for the Trinité River with the classification of the river segment from which the station originated. Overall percent misclassification is 53.8%.

	Number of observations and (percent) classified into:			
From:	I	II	III	Total
I	5	14	5	24
	(20.8)	(58.3)	(20.8)	(25.8)
II	8	27	5	40
	(20.0)	(67.5)	(12.5)	(43.0)
III	2	16	11	29
	(6.9)	(55.2)	(37.9)	(31.1)
Total	15	57	21	93
	(16.1)	(61.3)	(22.6)	(100.0)

TABLE 3. Discriminant analysis results for the habitat classification method described by Coté (1987) and Coté et al. (1986). Results shown are for the Trinité River with classification derived for the station specifically. Overall percent misclassification is 36.6%.

	Number of observations and (percent) classified into:			
From:	I	II	III	Total
I	14	21	0	35
	(40.0)	(60.0)	(0.0)	(37.6)
II	10	45	0	55
	(18.2)	(81.8)	(0.0)	(59.1)
III	0	3	0	3
	(0.0)	(100.0)	(0.0)	(3.2)
Total	24	69	0	93
	(25.8)	(74.2)	(0.0)	(100.0)

St-Jean and 22.9% for the Bec-Scie (data not shown). Trinité gives the most balanced proportion of stations from each category, and, having data from more years, will provide more reliable results. In the St-Jean River, only 3 stations out of 36 were originally classified as type II habitat and none were type III. All type II habitats were misclassified at type I, indicating that all areas sampled (and the river system) are highly uniform. In the Bec-Scie River, only 1 station out of 35 was originally classified as type III. The Trinité River had an approximately equal distribution of type I, II and III habitats. Overall, the greater proportion of the misclassifications are in the type II and III categories (Table 2). It appears that point estimates are either poor representatives of river segments, or that data from aerial photographs are too coarse-grained to render habitat quality data at specific sites.

If we apply the discriminant analysis to the classification at stations rather than at stream segments, the overall number of misclassified stations is reduced to 36.6% for the Trinité River (Table 3). In particular, 21 of 35 type I stations are misclassified as type II, 10 of 55 type II stations as type I and all (3) type III stations as type II. Differences among categories were significant overall (analysis of variance with all rivers pooled: R^2=0.326, F=39.0, df=2,161, P<0.0001). Furthermore, it seems that type I and II categories yield similar although significantly different densities of parr and fry (R^2 drops to 0.143, F=26.04, df=1,156, P<0.001), providing a basis for combining these 2 groups. Again, it appears that although the differences in densities between type I and II habitat may be significant, the large overlap in point estimates seem to indicate that in practical terms these groups have similar habitat uses.

Defining Patterns in Habitat Use

The variance explained by stream type (rapids, runs, flats, meanders, pools) is important. In the Trinité River, it explains 32.7% of the variance in total abundance (ANOVA, F=14.41, df=3,89, P<0.0001), while this value is 42.2% for Bec-Scie (F=7.80, df=3,32, P=0.0005) and 23% for St-Jean (F=10.14, df=1,34, P=0.0031), which had only 2 types of stream present. Among stream types, there are clear differences, both in terms of numbers and variances (Fig. 4). Runs have the highest densities, while rapids and flats follow, with pools having the lowest values. In terms of variance, runs are most variable, while rapids and pools are the least. It appears that stream type can be used effectively in defining a new classification system.

The relationship between bottom types and density of juveniles is difficult to establish for several statistical and biological reasons. Firstly, the relationship between substrate ratings and density is not necessarily linear, and may be curvilinear for mid-sized rocks (Fig. 5). Secondly, substrate ratings are calculated as percentage of total cover. Therefore, the

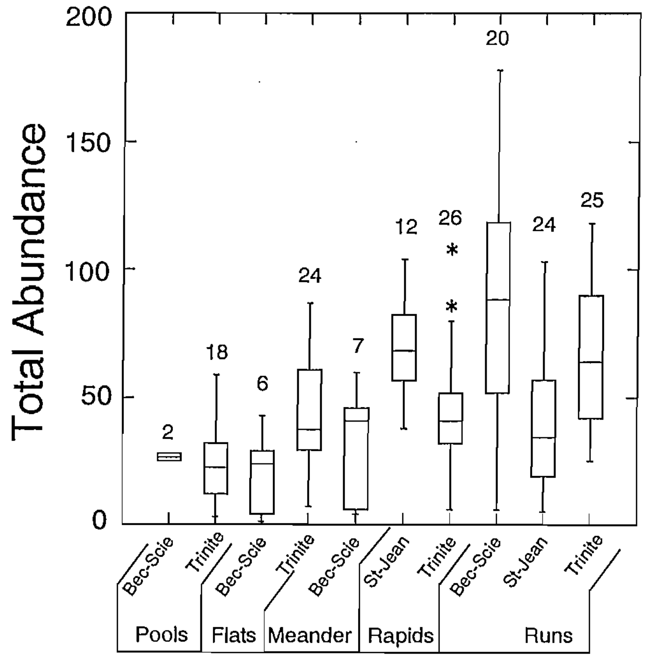

FIG. 4. Box plot of total juvenile abundance in relation to stream type from each river. The box plot is as in Fig. 2. There are clear differences in habitat use between stream types.

TABLE 4. Correlation matrix of substrate composition against Canonical factors (with Probability) for the 3 experimental rivers combined. The canonical factors are used in Fig. 6a and b.

Substrate composition	CAN1	CAN2	CAN3
Sand	0.483	−0.022	−0.088
	(0.0001)	(0.7374)	(0.1881)
Gravel	−0.166	0.001	−0.180
	(0.010)	(0.991)	(0.0051)
Pebbles	−0.460	−0.161	−0.065
	(0.0001)	(0.0101)	(0.299)
Cobble	−0.262	0.005	0.008
	(0.0001)	(0.928)	(0.900)
Boulders	0.484	0.355	0.107
	(0.0001)	(0.0001)	(0.0840)

sum of all ratings is always 100% and an increase in one type of substrate must be in concordance with the decrease of another. This is evident from the correlation matrix of substrate types, in which no positive correlations are found to be significant. For the same reason, the relationship of continuous variables with proportions is often difficult to model appropriately, especially if 0% and 100% values are frequent. Finally, bed types are not randomly distributed within stream type. In effect, a tight association exists that makes cause-and-effect resolution impossible.

These conclusions have been verified using canonical discriminant analysis (Fig. 6A,B, Table 4). This type of analysis is commonly used to represent associations between different types of data, like habitat qualitative data and population estimates (Jalbert et al 1989). From the data, it is evident that pools are associated with boulders and sand while meanders and runs are associated with pebbles, cobbles and gravel. Rapids are associated with boulders mostly and somewhat with sand while flats are neutral, not being associated with any particular bed type. This type of association between substrate type and stream type is not unexpected but limits hypothesis-testing under certain conditions. The presence of only certain stream types in particular rivers will also bias the representation of association from this type of analysis.

Overall, sand seems to be negatively associated with density (Fig. 5A), but this relationship is dependent on stream type. Again, there are 2 reasons for this: (1) Sand is not present in large quantities in rapids and runs, but can be 100% of bottom cover in pools; (2) A correlation analysis within stream types reveals that densities are not associated with any particular bottom types in rapids and runs but are significantly so in other stream types (Table 5). This is particularly true of sand, but positive associations with pebbles, gravel and small stones have also been noted. Association with cobble, pebbles and gravel also appears to plateau or begin to diminish at approximately 50% cover, even though the scatter is quite large (Fig. 5B, C, and D). Given this scatter, an increase in resolution of the classification method cannot be considered, with the exception of sand.

New Classification

The classification method derived in this paper is strictly a result of empirical exploratory analysis. Categories have been derived from population data collected from a series of stations. The behavioural preferences of salmon for certain micro-habitats from field or laboratory experiments is not used to refine the method. We chose this approach without making any assumptions about preferences and derived the classification from patterns in the data set.

From the data presented in this paper, it is apparent that runs and rapids are always well populated, and this is consistent among the 3 rivers. Analysis of correlations of total juvenile abundance with bed types within each stream type reveals no clear pattern or significant values for rapids and runs (Table 5), indicating that bottom type has no importance in these stream types, or that the range of bed types that could influence densities is not found within these habitats. Thus, strictly empirically, we classify these 2 stream types as new type "A" habitats, regardless of substrate composition.

Sand is the substrate category that is consistently important, in terms of its effect on local abundance, particularly in pools and flats (Table 5). The effect of sand in all stream types other than rapids and runs seems to become noticeable at about 10% cover, while 35% cover or more is associated with drastically decreased abundance (Fig. 5A). These conclusions must be taken carefully, however, because almost all variation in sand concentration (except for 2 stations in the Bec-Scie River) is found in the Trinité River.

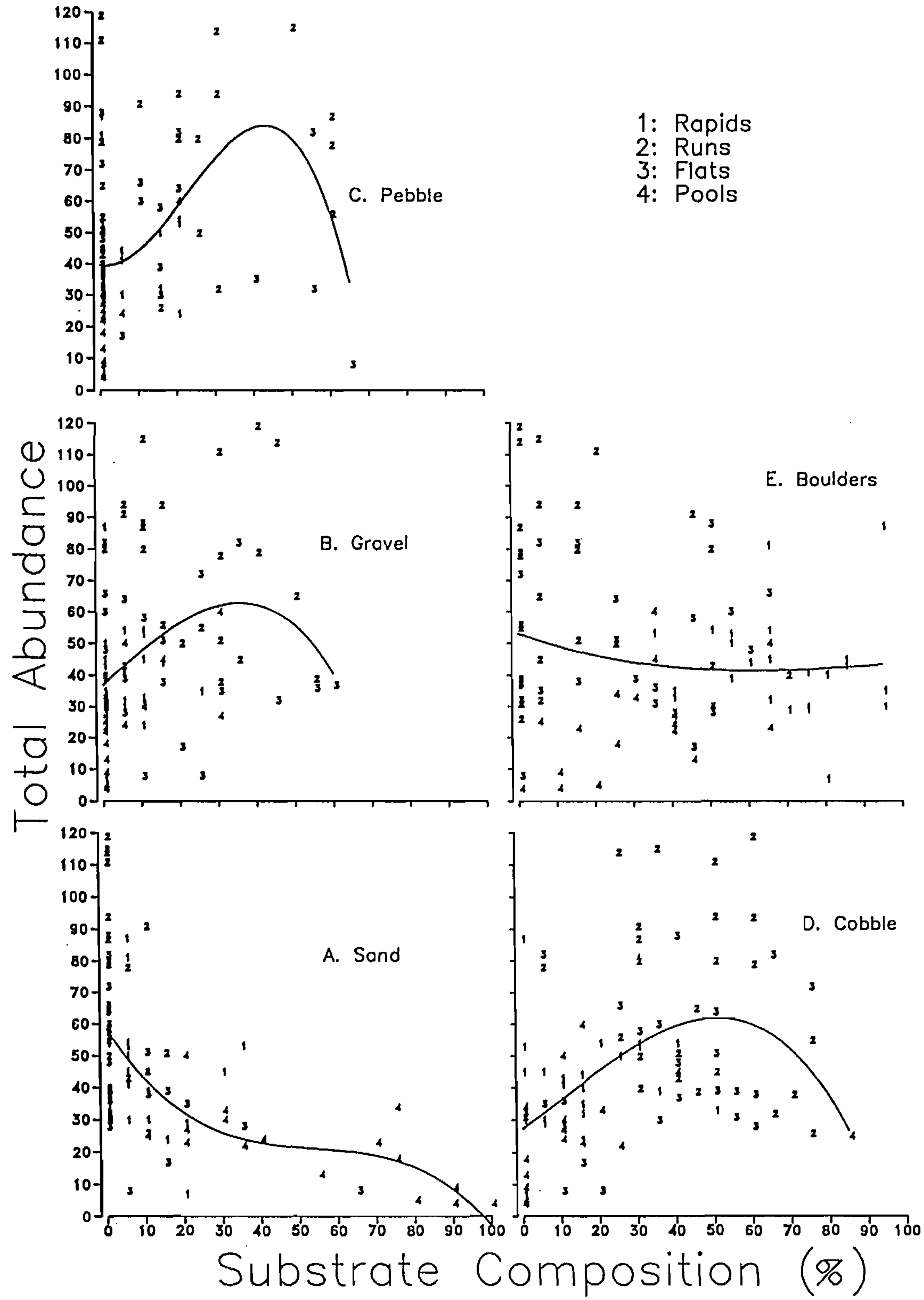

FIG. 5. Bivariate representation of total juvenile abundance in relation to substrate composition, for each of the 5 categories. The data is from the Trinité River. The line is a fitted 3rd order polynomial. It is used only to indicate possible trends in the data. The data points represent a station-year and the number indicates stream type. Sand is clearly unsuitable substrate for juvenile salmon, while gravel pebbles and cobbles seem to peak at 40 to 55% cover. Although patterns emerge when explored within size groups, the groups remain artificial and may mask interaction effects between substrate of various coarseness.

As the purpose of this technique is to determine habitat quality in initial stream surveys, the classification of all stream segments other that runs or rapids that contain any quantity of sand might be best classified as type "B". All habitats, including rapids, runs, pools and flats that do not contain sand are classified as type "A". Figure7 demonstrates the differences in densities observed in rapids, runs, pools and flats when sand is present and absent for the Trinité River data. The difference in density within rapids/runs is not significant (ANOVA, Rapids: F=0.038, df=1,24, P=0.848; Runs: F=1.443, df=1,23, P=0.242). Although the sample size for pools without sand is limited to 1 station, overall the effect is clearly visible (ANOVA excluding rapids/runs, R^2=0.349, F=21.447, df=1,40, P<0.0001).

The new classification criteria of 0% sand for stream types other than rapids/runs have been verified. Using discriminant analysis, only 16.13% of stations were misclassified (Table 6). If the 10% threshold for sand is used instead of 0%, the estimate of misclassification remains the same (data not shown). Furthermore, if the 10-35% sand cover is used as threshold for a new middle category, yielding 3 classes ("A", "B", and "C"), the classification fails overall 20.43% of the time (data not shown). It is interesting to note as well that in this particular classification system, most type B stations are misclassified as type A, strengthening our belief that 2 categories are adequate.

Given the simplicity of classification by simple presence or absence of sand, the method is ideal for rapid estimation of the suitability of rivers to salmon enhancement or production. Figure 8 gives the results of the classification method proposed here. There is an apparent uniform density and variance of abundance within each grouping for all rivers, and the difference in the mean densities between the 2 groups

TABLE 5. Pearson correlations (and probabilities) of total juvenile salmon abundance with substrate composition within stream types, for the Trinité River. Substrate composition is arsine square root transformed proportions. Total abundance are log transformed. Significant correlations are in bold.

Substrate Composition	Pools (n=18)	Flats (n=24)	Rapids (n=26)	Runs (n=24)
Sand	**−0.81 (0.0001)**	**−0.62 (0.0013)**	−0.20 (0.3359)	−0.31 (0.1457)
Gravel	**0.53 (0.0225)**	−0.17 (0.4355)	0.13 (0.5292)	0.26 (0.2161)
Pebbles	0.33 (0.1756)	−0.06 (0.7773)	0.09 (0.6477)	0.28 (0.1916)
Cobble	**0.55 (0.0177)**	0.35 (0.0929)	0.21 (0.3145)	−0.32 (0.1296)
Boulders	**0.63 (0.0049)**	0.33 (0.1184)	−0.04 (0.8544)	−0.03 (0.8946)

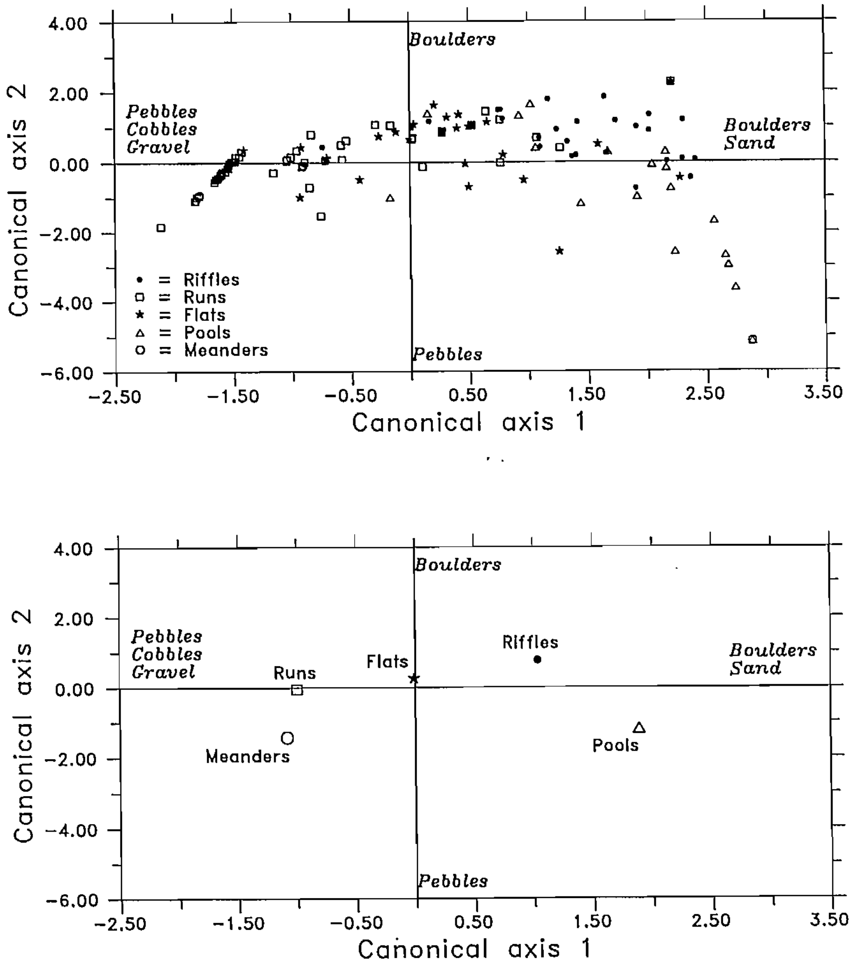

FIG. 6. Multiple canonical discriminant analysis separating the various stream habitats according to their association with different substrate composition. A: Individual stations. B: Stream habitat means.

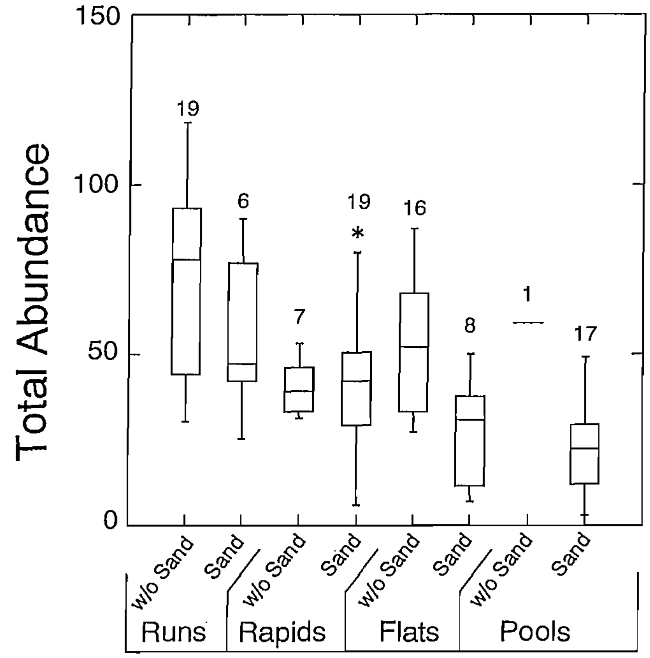

FIG. 7. Box plot of total juvenile abundance with combination stream type and sand groupings. The sand groupings represent simple presence or absence. The box plot is as in Fig. 2. The difference within rapids and runs is not significant (see text), but is highly so for flats and pools pooled.

TABLE 6. Discriminant analysis results for the new classification method described in the text. Results shown are for the Trinité River and for classification of station data. Overall misclassification rate is 16.13%.

From:	Number of observations and (percent) classified into: A	B	Total
A	66 (95.6)	3 (4.4)	68 (73.1)
B	12 (48.0)	13 (52.0)	25 (26.9)
Total	77 (82.8)	16 (17.2)	93 (100.0)

is large (All rivers, years and stations combined, ANOVA, $R^2=0.256$, $F=55.61$, df=1, 162, $P<<0.0001$). By using the simple presence or absence of sand in pools and flats as the threshold level in the classification process, the loss in accuracy to a more precise quantitative estimate of sand cover, when compared to the time required to estimate cover, is perhaps negligible.

Discussion

The classical method of classification of salmon habitat is a valuable tool but fails to classify juvenile densities from station data, perhaps because of the complex bed type interaction thought to influence juvenile salmon density. According to the results from the experimental rivers, it is apparent that juvenile salmon are much less selective of habitat criteria than originally thought, and that productivity of the river may contribute much more to the variance in density than availability of particular forms of habitat. The high level of misclassification of type I and II habitats is congruent to the idea that only usable and non-usable habitats must be distinguished to estimate egg deposition rate, and that any increase in accuracy of the model is not done in concordance with an equivalent increase in precision.

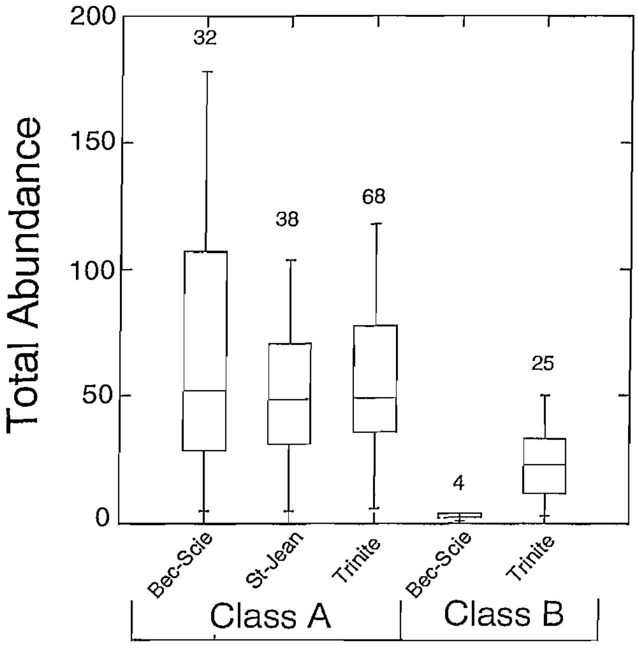

FIG.8. Box plot of the result of the new classification method described in the text. Box plots are as in Fig. 2. The difference between class A and B habitats is highly significant (see text).

The relatively small variances associated with rapid and run stream types are predictable from the life history and behaviour of juvenile salmon. Parr are known to be territorial in rapids and runs. Grant and Kramer (1990) have shown that territory size of salmonids determines maximum density in shallow habitat, but that territorial behaviour may break down and other forms of social interaction may prevail in deeper waters. Presence of sand is strongly negatively associated with density. However, it cannot be assumed that sand has a direct impact on habitat use without experimental manipulation. Alexander and Hansen (1986) observed a net reduction of brook trout biomass with an experimental introduction of sand into a trout stream. They report that a relatively small sand bedload had a marked effect on trout and their habitat. Moving sand is the least desirable bed type for benthos, having a major impact on food production (Alexander and Hansen 1986). It is also possible that the presence of sand reduces the availability of micro-habitat favourable to salmon. It appears from the literature that a mixture of habitats is better than a homogeneous river, but the validation of such viewpoint is only possible on theoretical grounds. Convoluted bedrock, that is bedrock which has many pits, depressions, projections and fractures can provide a fairly good substrate for some invertebrates and fish, whereas smooth bedrock does not. Convoluted bedrock was present in 2 stations in the Bec-Scie River.

Even with the new classification method, it is apparent from the data that habitats that are classified as type "B" are capable of holding large numbers of parr or fry. This is demonstrated by the error rate of 48% in classification of type "B" habitats in Table 6. Talbot and Myers (in prep) have found supporting evidence for the niche expansion theory for juvenile salmon from analysis of time-series data on habitat use. They have concluded that secondary or tertiary habitats can be used by salmon when overall population abundance is high, but tends not to be used when overall populations are low. This type of marginal expansion of habitat suitability has also been described in other studies (birds: Rice et al. 1986, Van Horne 1983; aphids: Whitham 1980).

The classification system is somewhat complicated by the inter-year variance in the population estimates. It may happen that population estimates are low in one year of a series of several. This may be due to sampling variance or to some ecological factor, but may indicate a poor habitat when the time-series reveals that it actually is not. In such circumstances, it may be better to use the year with the best population estimate in a time-series for a particular station, or to work with some method of eliminating aberrant years.

The method presented here has been reduced systematically to the simplest components of habitat selection, whether passive or active. It would be a useful exercise to further model interaction of substrate composition groupings. Improved precision in the prediction of standing stock may be an asset in certain circumstances. Other critical elements that cannot be ignored in estimating production from habitat includes habitat-specific growth rates, mortality rates and biomass.

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The Development of Habitat Suitability Curves for Juvenile Atlantic Salmon (*Salmo salar*) in Riverine Habitat in Insular Newfoundland, Canada

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Generalized habitat suitability indices are developed for juvenile Atlantic salmon from data for 18 rivers (242 stations) in insular Newfoundland, Canada. Habitat variables used to develop suitability curves included mean stream width, mean station depth, station velocity, station discharge, proportion of instream and overhanging cover, ice scar height, and proportions of substrate types. Histograms, with smoothing techniques, were used to develop a curve to relate the indicator variable (number of fish per 100 m^2) to the range in each habitat variable. Suitability indices for Atlantic salmon fry were consistent, suggesting a well defined set of habitat preferences. Parr habitat suitability curves demonstrated more variability with the most consistent curves for the variables stream width, mean depth, and discharge. The curves developed in this paper are discussed with respect to their potential use for management of freshwater habitat and assumptions and limitations that may constrain their application as a tool for habitat evaluation.

Les auteurs ont calculé des indices généralisés de caractéristiques de l'habitat favorables aux juvéniles de saumon de l'Atlantique à partir de données obtenues pour 18 cours d'eau (242 sites) de l'île de Terre-Neuve (Canada). Les variables de l'habitat utilisées pour l'élaboration des courbes comprenaient la largeur moyenne du cours d'eau, la profondeur moyenne, la vitesse du courant et le débit aux stations, de même que les proportions de couvert en cours d'eau et surplombant, la hauteur atteinte par les glaces et les proportions des types de substrats. Des histogrammes, traités par techniques de lissage, ont servi à dresser des courbes établissant une relation entre la variable de l'indice (nombre de poissons par 100 m^2) et la gamme de chaque variable de l'habitat. Les indices des caractéristiques favorables de l'habitat pour les alevins étaient cohérents, ce qui porte à croire à l'existence d'une ensemble bien défini de préférences. Les courbes obtenues pour les tacons présentaient une plus grande variabilité, les plus uniformes étant celles des variables ayant trait à la largeur, à la profondeur moyenne et au débit des cours. Les auteurs traitent des courbes obtenues dans le contexte de leur application à la gestion des habitats d'eau douce et font état des hypothèses et des limitations qui pourraient en restreindre l'utilisation comme outil d'évaluation des habitats.

Introduction

Habitat suitability curves (indices) are a representation of the relationships between a species and the habitat variables believed to be important to the well being of that species. Habitat suitability indices (HSIs) or curves (HSCs), based on individual or aggregated habitat parameters, have been developed and used extensively in evaluating potential impacts of habitat alterations for aquatic and terrestrial species (Armour et al. 1984). Habitat suitability is the relationship between a species and habitat variables believed important to the growth, survival, standing crop (population density), or other expression of the well being of that species (Bovee and Zuboy 1988). The mathematical expression of the relationship varies from 1.0 (optimum habitat condition for the variable) to 0.0 (unsuitable habitat with minimal/no potential for use by the species). HSIs for a variety of important variables can be aggregated into an overall suitability index (SI) through a habitat suitability index model. Habitat suitability indices and models are employed to simplify habitat/species relationships and to develop tools to apply existing knowledge to problem solving (e.g., habitat management decisions). Suitability criteria have inherent assumptions and limitations and these must be clearly understood and considered by developers and users of habitat suitability criteria.

Currently, freshwater fish habitat in Newfoundland and Labrador is managed predominantly in a quantitative sense (number of habitat units) with general qualitative considerations (e.g., habitat types, general quality of the habitat). Qualitative considerations are subjective leading to lack of standardization in decision making between projects, individuals charged with making evaluations, and geographical regions. A need exists to develop habitat evaluation methodologies to effectively determine habitat losses/gains to ensure conservation of the productive capacity of fish habitat. Any habitat evaluation approach must offer flexibility and alternatives in finding solutions for compensation or mitigation. Habitat suitability indices have been used extensively in evaluations of potential impacts of projects on fish habitat and a number of habitat suitability index (HSI) models for aquatic and terrestrial species have been developed (Shirvell 1989). In this paper, we explore the development of a suite of indices for Atlantic salmon (*Salmo salar*) and discuss their potential uses.

In this paper, habitat suitability indices are developed for Atlantic salmon juveniles (fry and parr) from fish population and habitat (macrohabitat) attribute data collected from sampling stations on a diverse set of insular Newfoundland rivers. The suitability criteria developed in this paper are discussed with respect to their ecological significance, potential use for freshwater habitat management, and assumptions and limitations that constrain their potential application.

Methods

The data set employed in the development of habitat suitability relationships (curves) for juvenile Atlantic salmon included fish abundance and habitat attribute data from 242 stations from 18 rivers in insular Newfoundland, collected over the period 1980 to 1988. Table 1 contains a listing of rivers, number of stations, and the sampling period. The complete data set was considered as 2 data sets; one containing all stations from 18 rivers (ALL, n=242 stations, Table 2) and a geographical subset for 4 rivers in the Experimental Rivers Program, southeast Avalon Peninsula (EXP. RIV., n=156 stations, Table 3). The indicator variable used in curve development was numbers of fish of a life stage (fry or parr) per unit of habitat (100 m^2). Parr were not partitioned into size and/or age groups. Fish were collected from stations ranging from 52 to 657 m^2 (0.52 to 6.57 units) by electrofishing, seining, or combinations of the two methods. Numbers of fish per habitat unit were actual total catches and were not estimates of population size (the use of population estimates would have severely reduced the data set owing to the absence of estimates for each age group).

Habitat attributes used in data analysis included measurements of stream width, depth (mean and maximum), velocity (mean and surface), instantaneous discharge, cover (instream, overhanging, and canopy), ice scar (scour) height, and proportions of substrate types. All habitat variables were collected at the time of fish sampling. Data used were mean values for each station (e.g., width, depth, velocity, ice scar height) or data representing proportions for the entire station area (e.g., percentages of cover types, substrates) and were not microhabitat variables associated with individual fish. Details on collection of habitat variables are contained in Gibson et al. (1987).

TABLE 1. Rivers and dates sampled for fish abundance and habitat attribute data used for development of habitat suitability relationships for Atlantic salmon. Rivers in the Experimental Rivers (EXP. RIV.) subset are identified with an *.

Name	*N*	Sampling Period
Gander River	2	06–1980
Anchor Brook	3	07 to 08–1983
Deadmans Brook	3	07 to 08–1983
Northwest Brook (BB)	6	08–1982
Southwest Brook	10	08–1981 to 08–1982
Wings Brook	24	08–1981 to 08–1983
Salmon Brook	1	08–1982
Southwest River	1	09–1982
North Arm River	7	06–1980 to 07–1983
*Freshwater River	71	05–1984 to 08–1988
*Long Beach River	5	08–1985 to 08–1988
*Northeast Trepassy River	57	05–1984 to 08–1988
*St. Shotts River	1	08–1985
*Tides Brook	5	07 to 08–1983
Big Salmonier Brook	1	08–1983
Highlands River	16	05–1980 to 07–1981
Western Arm Brook	6	07–1980

TABLE 2. Summary of habitat attributes and fish abundance data from the large data set (ALL). Fish densities (numbers/100 m² are in the shaded block.)

Variable	N	Minimum	Maximum	Mean	Std. Dev.
Discharge ($m^3 \cdot s^{-1}$)	224	0.00	2.47	0.52	0.41
Area (m^2)	230	38.08	657.90	219.17	134.22
Width (m)	230	1.70	21.30	7.70	3.41
Depth (cm)	227	8.00	65.00	22.54	10.17
Maximum Depth (cm)	212	20.00	194.00	52.43	25.71
Mean Velocity ($m \cdot s^{-1}$)	226	0.00	0.87	0.31	0.17
Surface Velocity ($m \cdot s^{-1}$)	45	0.00	0.76	0.25	0.19
Pool Length (m)	124	0.00	43.10	7.23	12.75
Number of Pools	133	0.00	3.00	0.39	0.64
Ice Scar Height (cm)	66	0.00	335.00	83.08	67.87
Instream Cover (%)	177	0.00	99.00	18.89	21.91
Overhanging Cover (%)	192	0.00	75.00	7.84	13.09
Canopy Cover (%)	156	0.00	50.00	3.21	9.01
Fines (%)	222	0.00	100.00	4.53	13.30
Gravel (%)	222	0.00	90.00	6.30	12.97
Pebble (%)	222	0.00	90.00	12.00	14.33
Cobble (%)	222	0.00	90.00	32.26	20.11
Rubble (%)	222	0.00	90.00	27.62	17.70
Boulder (%)	222	0.00	100.00	17.18	18.54
Bedrock (%)	222	0.00	25.00	0.11	1.68
Substrate Rating	233	0.00	233.00	121.61	34.91
Water Temperature (°C)	210	1.70	27.00	17.29	3.98
Conductivity ($\mu S \cdot cm^{-1}$)	109	18.00	248.00	72.25	62.09
Fry	181	0.18	153.69	21.92	31.98
Parr (1+)	210	0.19	90.94	21.44	19.04
Parr (2+)	205	0.36	64.56	9.88	10.95
Parr (3+)	139	0.15	26.25	3.30	3.70
Parr (4+)	31	0.19	4.42	1.25	1.10
Parr (total)	230	0.0	122.35	30.55	24.85
Total (all juvenile salmon)	230	0.58	202.59	47.80	41.17

TABLE 3. Summary of habitat attributes and fish abundance data from the Experimental Rivers data set (EXP. RIV.). Fish densities (numbers/100 m^2 are in the shaded block.)

Variable	*N*	Minimum	Maximum	Mean	Std. Dev.
Discharge ($m^3 \cdot s^{-1}$)	154	0.00	1.51	0.49	0.33
Area (m_2)	156	38.08	657.99	204.13	131.23
Width (m)	156	1.70	15.40	7.92	3.30
Depth (cm)	154	8.00	59.00	21.84	9.80
Maximum Depth (cm)	150	20.00	194.00	51.93	26.94
Mean Velocity ($m \cdot s^{-1}$)	156	0.0	0.87	0.31	0.18
Surface Velocity ($m \cdot s^{-1}$)	28	0.00	0.76	0.20	0.18
Pool Length (m)	106	0.00	43.10	5.93	12.84
Number of Pools	115	0.00	1.00	0.22	0.41
Ice Scar Height (cm)	43	0.00	162.00	61.63	48.18
Instream Cover (%)	141	0.00	99.00	20.62	23.34
Overhanging Cover (%)	137	0.00	60.00	6.01	10.01
Canopy Cover (%)	131	0.00	50.00	2.63	8.30
Fines (%)	152	0.00	50.00	3.28	8.13
Gravel (%)	152	0.00	20.00	4.09	4.71
Pebble (%)	152	0.00	60.00	12.73	11.46
Cobble (%)	152	0.00	75.00	32.55	16.78
Rubble (%)	152	0.00	75.00	29.07	15.56
Boulder (%)	152	0.00	75.00	18.28	16.95
Bedrock (%)	152	0.00	0.00	0.00	0.00
Substrate Rating	152	59.45	202.67	125.98	28.45
Water Temperature (°C)	145	1.70	23.50	17.17	3.70
Conductivity ($\mu S \cdot cm^{-1}$)	66	18.00	232.00	54.24	49.78
Fry	121	0.20	153.69	28.48	36.14
Parr (1+)	136	0.19	90.94	23.59	20.60
Parr (2+)	132	0.38	64.56	11.44	12.71
Parr (3+)	89	0.15	26.25	4.06	4.32
Parr (4+)	18	0.38	4.42	1.44	1.22
Parr (total)	156	0.00	122.35	32.70	26.96
Total (all juvenile salmon)	156	0.58	02.59	54.79	44.82

All habitat attribute data were treated as collected (i.e. no transformations) with the exception of proportion of substrate types. It was necessary to combine the proportions of the different substrate types within each station into one measure or index. A weighting scheme rating each substrate type in relation to coarseness, as determined from $\log_{10}$ of the mean particle size, was adopted as follows:

(1) coarseness rating = $\log_{10}$ (mean particle size + 1)

The coarseness rating for each substrate type was multiplied by the proportion (%) of each type in the station and the totals for gravels, pebble, cobble, rubble, and boulders were summed to give an overall rating for the station. Bedrock and fines (sands through organic detritus) were considered unsuitable substrates and were not included in determining a suitability function for coarseness rating.

Frequency analysis (histograms), relating the indicator parameter (# fish/unit area) to the range in each habitat variable, was used to express habitat preference or suitability (Bovee and Cochnauer 1977). The interval size used to express suitability for each variable was established in relation to the sample size and range in values, as recommended by the U.S. Fish and Wildlife Service (Cheslak and Garcia 1988; Sommerville 1958). Preference curves were constructed using the (common) average performance approach (Bovee 1986) and were developed separately for two life stages of salmon; fry (YOY, young of the year, juveniles during their first summer of life) and parr (PARR, juveniles during their second to fourth year of life). The range (or interval) of each habitat variable most frequently used by each life stage is considered optimum habitat and was assigned a habitat suitability of 1.0 while all other values were assigned a suitability index between 1.0 and 0.0 based on relative frequency. The suitability curve was constructed by connecting the corners of the bins expressing suitability of 1.0, drawing a line to the mid-point of adjacent bins, and extending the curve to the end of the data range on the tail(s) of the distribution (Slauson 1988). In several cases, the suitability curve was extended in the lower data range to a '0' value. This does not imply correspondence between a 0 value for a given habitat attribute and a preference rating but rather is an artifact of using histograms to construct the curve. Curve smoothing using a 3-way running mean filter (no more than two passes) was applied, where appropriate, to assist in defining monotonic or unimodal curves (Bovee 1986). Curves developed from individual data (observations of individuals in relation to a habitat variable) require determination of both habitat use and habitat preference (habitat use adjusted in relation to availability). In this study, the indicator variable is adjusted relative to available habitat (divided by the station area) consequently, the resulting curves reflect habitat suitability or preference.

Results

A statistical summary of habitat attribute and fish abundance data for the two data sets is listed in Tables 2 and 3. Initially, the distributions of the habitat variables used to define habitat availability were compared statistically using the Wilcoxon Rank Sum test (SAS Institute Inc., 1985). The test indicated (at p=0.10) that the distribution of the habitat variables in the two data sets was not significantly different for many habitat attributes (12 of 23) excepting the variables area, discharge, maximum depth, ice scar height, pool number, pool length, overhanging cover, canopy cover, % gravel, % pebble, and substrate rating. The seven fish abundance variables were not significantly different (at p=0.10).

Suitability curves for fry and parr were developed for eight habitat variables for both data sets. Curves for stream width and mean depth are contained in Fig. 1, mean velocity and discharge in Fig. 2, ice scar height and substrate rating in Fig. 3, and instream and overhanging cover in Fig. 4. Five variables are measures of morphometric/hydrological conditions (width, depth, velocity, discharge, ice scar height) while the other three attributes are cover variables (instream cover, overhanging cover, substrate rating).

Width

The fry suitability curves (Fig. 1) for station width demonstrated a preference for small streams (optimum suitability at values <2.5 m and rapid decline in suitability after that interval) with stream widths greater than 17.5 m demonstrating poor suitability. The parr curves (Fig. 1) are similar with a wider optimum range (0.0 to 5 m) and more gradual decline in suitability. Suitability curves for both data sets were consistent with the extended tail of the parr curve (ALL data), a result of having a wider range of values from which to develop the curve

Depth

Fry curves for mean (station) depth (Fig. 1) demonstrated optimum suitability in the range 15 to 20 cm with steady declines in suitability for depths greater than 20 cm. The optimum depth range for the parr curve was 15 to 25 cm and HSIs demonstrated more gradual decline at values greater than 25 cm (deeper stations). Curves for both life stages demonstrated sharp declines in suitability in the lower (shallower) ranges (< 10 cm). Curves for both data sets were similar with the parr curve from the EXP. RIV. demonstrating higher suitability values at depths greater than 25 cm.

Velocity

Velocity suitability curves (Fig. 2) for both fry and parr demonstrated a wide range in optima reflecting a flat response to mean station velocity. Optimum fry

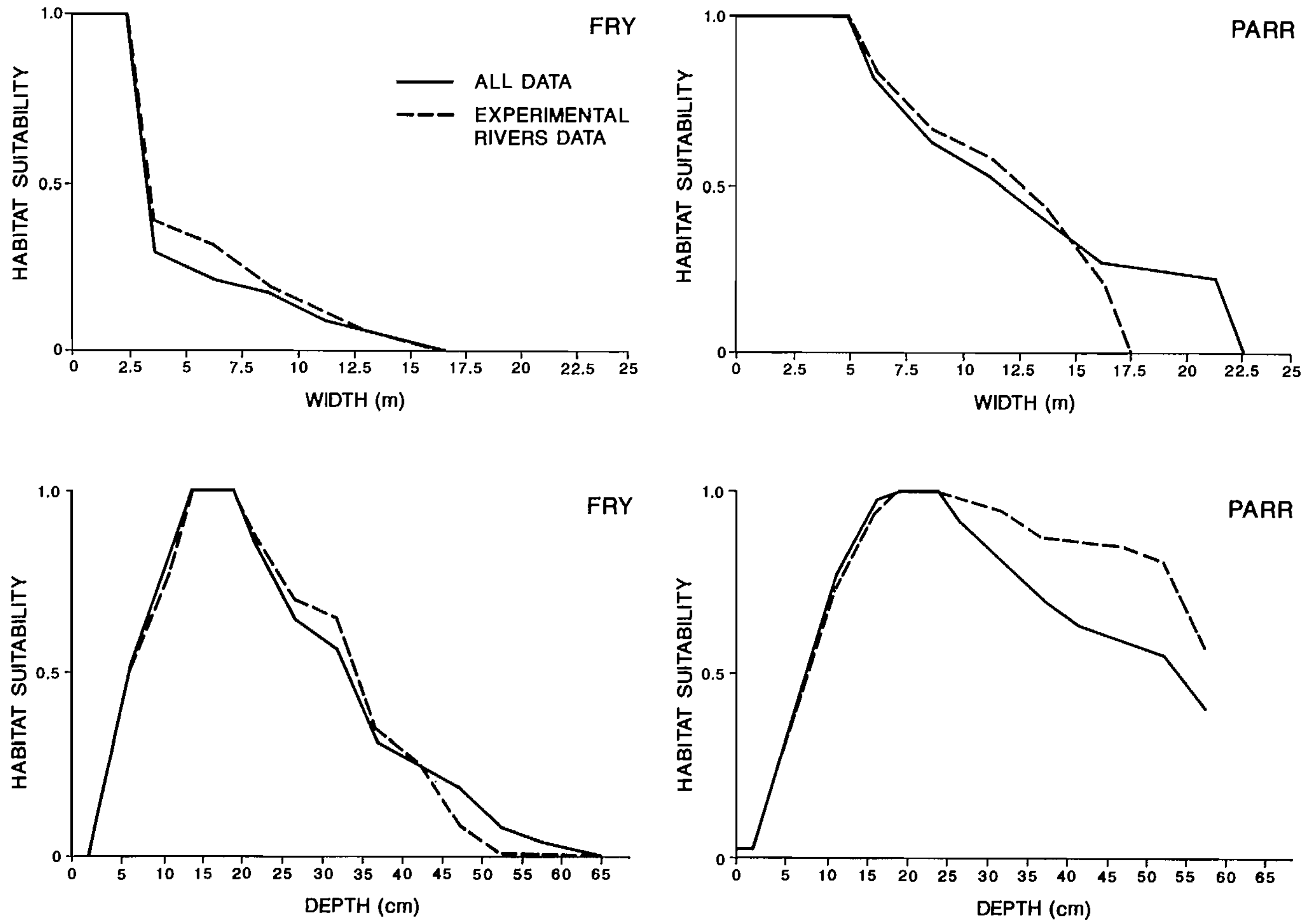

FIG. 1. Habitat suitability curves for Atlantic salmon fry and parr in relation to stream width and mean depth.

suitability ranged from 0.20 m·s^{-1} to 0.60 m·s^{-1} (0.70 m·s^{-1}, EXP. RIV.) with sharp decline on either end of this range. Optimum parr suitability was in the range 0.10 to 0.50 m·s^{-1} with declines at velocities greater than 0.50 m·s^{-1}. Parr demonstrated higher suitability (0.79) than fry (0.25 to 0.33) in the lower velocity range (0 to 0.10 m·s^{-1}). Curves developed from both data sets were consistent in shape and range of optima, excepting the sharp decline in parr suitability at velocities greater than 0.5 m·s^{-1} for EXP. RIV.

Discharge

Discharge suitability curves for both life stages (Fig. 2) demonstrated similar shape and range of optima. Preferred discharge was at the low end of the range, 0.0 to 0.25 m^3·s^{-1}, with a steady decline above this range. Both life stages reflected HSIs less than 0.5 above a discharge of 1.25 m^3·s^{-1}. Curves developed from both data sets were similar, however, the tail of each curve diverged at discharges greater than 1.25 m^3·s^{-1}.

Ice Scar Height

Suitability curves for ice scar height (proxy variable for range of discharge or 'flashiness') demonstrated similar range of optima and trends for both fry and parr for ALL data (Fig. 3). Optimum suitability was evident in the lower ranges (0 to 150 cm) with declining suitability above 150 cm. Fry HSIs demonstrated a steep decline over the higher values while parr response was more gradual and relatively flat. Curves developed from the EXP. RIV. data set (Fig. 3) were markedly different from those for the large data, set reflecting the narrow range values of ice scar height in the data subset. Optimum parr suitability (EXP. RIV.) was in the 100 to 150 cm range and for fry in the range from 50 to 100 cm.

Substrate Rating

Fry suitability curves (Fig. 3) for substrate (rating for coarseness) demonstrated optima in the range 100 to 125 which would indicate preference for pebble/cobble-dominated stations. Suitability indices in the range lower than the optima (finer substrates) declined rapidly while in the higher ranges HSI declined more slowly with a sharp decline above 225 (boulder-dominated sites). Parr suitability curves (Fig. 3) demonstrated increasing preference with increasing coarseness to reach optimum at the highest range (> 225, boulder-dominated sites) for ALL data. The parr curve for the EXP. RIV. demonstrated a flat response with optima across the range in substrate rating from 50 to 175, reflecting the narrower range in substrate rating values and absence of stations with substrate coarseness ratings at either end of the distribution in the data subset.

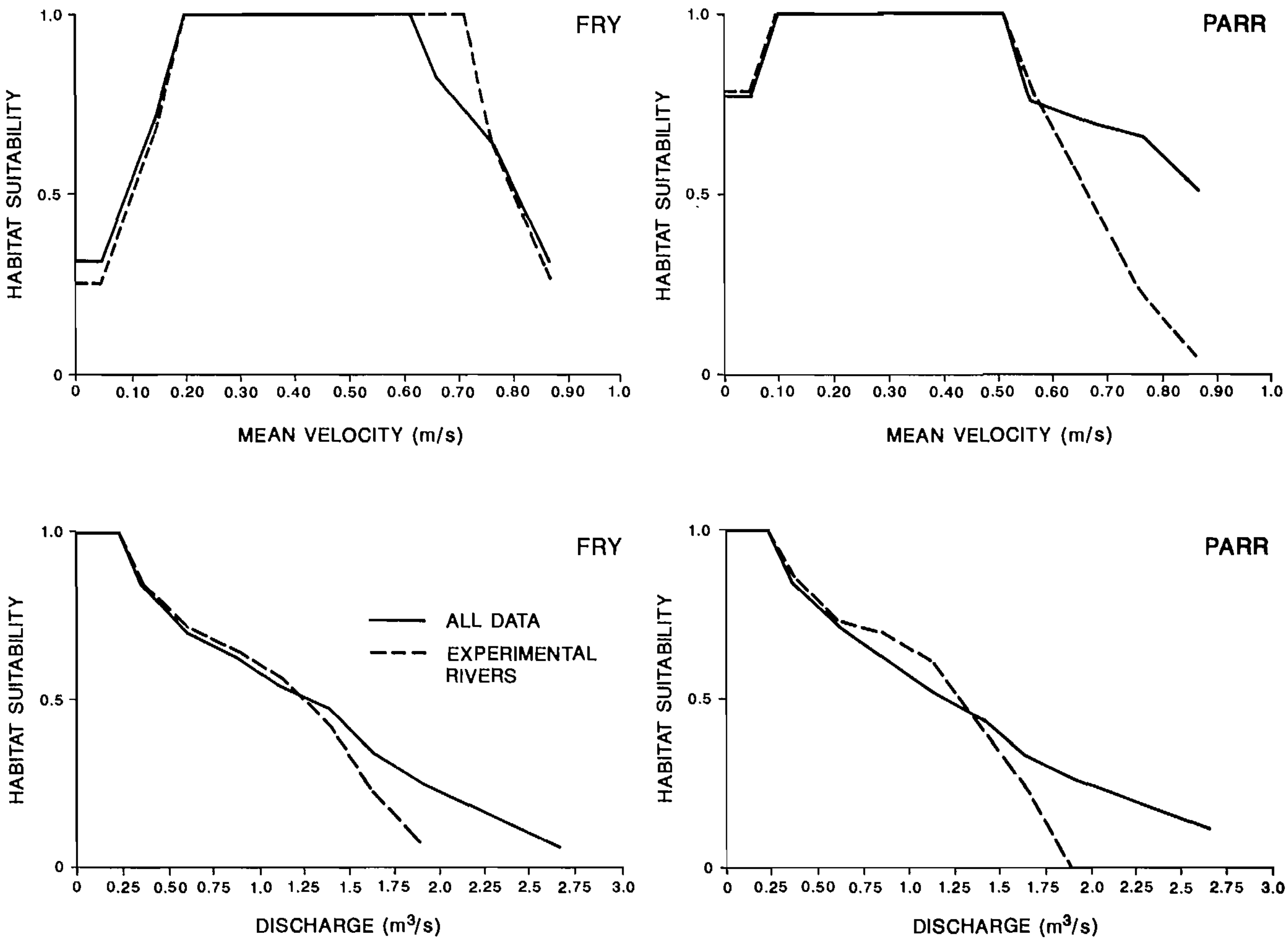

FIG. 2. Habitat suitability curves for Atlantic salmon fry and parr in relation to mean velocity and discharge.

Instream Cover

Fry curves for instream (Fig. 4) cover demonstrated optimum suitability from 0 to 10% with a gradual decline above this range to reach 0.42 (0.38 for EXP. RIV.) at 100%. The parr curves (Fig. 4) demonstrated a wide range in optimum which is evidence of flat response to instream cover. Parr curves demonstrated less than optimum suitability in the lower ranges and a sharp decline above 80% instream cover. Curves developed from both data sets for both life stages were similar.

Overhanging Cover

Fry curves for overhanging cover (Fig. 4) demonstrated optima in the lower ranges (0 to 30% for ALL, 0 to 10% for EXP. RIV.) with steady declines in suitability above the optimum. The shape and trend in the fry curves for both data sets were similar. The parr curve for ALL data (Fig. 4) demonstrated a flat response with optimum values over a wide range (0 to 60%). The parr curve for the EXP. RIV. (Fig. 4) was markedly different and had an optimum range from 60 to 70%, with sub-optimum HSIs in the lower ranges to reach a minimum of 0.46 from 0 to 25% overhanging cover

Discussion

Habitat suitability indices were developed from diverse rivers/habitats in insular Newfoundland for width, depth, discharge, ice scar height and substrate coarseness rating. The wide range in optima for velocity and cover variables (instream, overhanging) suggest that these curves will require refinement or, conversely, that these variables are of lesser importance in determining habitat selection by juvenile salmon in insular Newfoundland. Fry suitability curves for the two data sets were remarkably consistent, suggesting a well-defined set of habitat preferences for salmon fry. Parr curves between data sets were not nearly as consistent and this result suggests that parr are more plastic in their habitat requirements or possibly that other influences have obscured habitat preference (e.g., competition or available habitat). It might also indicate that selection of habitat changes as parr grow and that separate suitability curves may be required for different size/age ranges. Additionally, due to low numbers of freshwater fish species in insular Newfoundland, juvenile salmon are able to utilize a wider range of habitats than they do in other parts of their distribution (deGraff and Bain 1986).

The most consistent suitability criteria were evident for the attributes stream width, mean depth, and

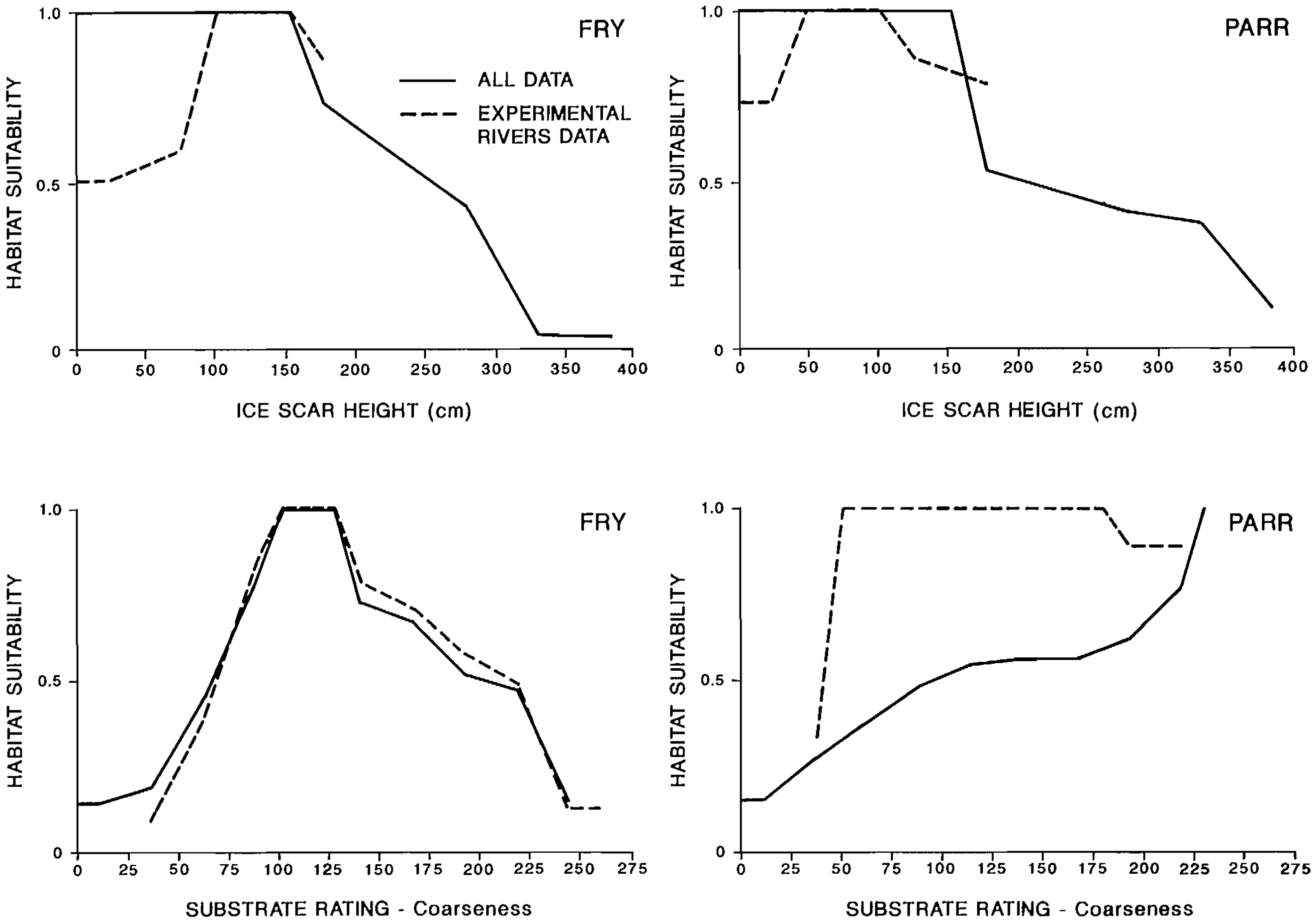

FIG. 3. Habitat suitability curves for Atlantic salmon fry and parr in relation to ice scar height and substrate rating.

discharge. These variables are related to stream order with width, depth, velocity and discharge tending to increase as stream order increases (Vannote et al. 1980; Platts 1979) and curves presented in this paper are consistent with these considerations. Hydrological variables (e.g., discharge) have been shown to be reasonable indicators of other habitat characteristics and have been related to juvenile salmon production (Chadwick 1982; Frennette et al. 1984), with production demonstrated to be higher in smaller, headwater streams (Gibson et al. 1987; Gibson 1990). Gibson et al. (1990), in rivers on the southeast Avalon Peninsula, found the most productive juvenile salmon habitat to be small streams with stable discharge and coarse substrate. Parr densities on these rivers were most influenced by substrate and stream width. Keenleyside (1962) also found fry and parr abundance to be greater in upper reaches of rivers. However, we found that parr are more abundant in wider streams than those generally preferred by fry, which is consistent with the tendency for parr to disperse to use a wider diversity of habitat as they grow and demonstrate territorial behaviour in flowing water with requirements for larger territories (Gibson et al. 1990).

The relatively flat response of juvenile salmon to velocity (wide range of optima) demonstrated in this paper is likely not indicative that this variable is unimportant in habitat selection; conversely there is a wealth of literature as to velocity influence on habitat selection (Wankowski and Thorpe 1979; Symons and Heland 1978; Gibson et al. 1990). Heggenes (1990) found mean or surface water velocities to be the most important variable determining habitat selection, often in combination with substrate. Morantz et al. (1987), in Nova Scotia and New Brunswick rivers, found substantial overlap in velocities selected by fry and parr with fry preferenda ranging from 5 to 10 cm·s^{-1}, small parr (< 100 mm) from 7 to 15 cm·s^{-1}, and large parr (> 100 mm) from 10 to 20 cm·s^{-1}. They concluded that juvenile salmon tolerated a wide range in depth and substrates and that water velocity, at the holding position (nose velocity), was the dominant factor influencing habitat selection. DeGraff and Bain (1986) have also previously demonstrated a broad range in optimum velocity and utilization for fry and parr in preference curves developed for two Newfoundland rivers. These authors suggest that lack of competition from other species (in the study rivers and insular Newfoundland in general) has permitted more extensive use of available habitat types, reflected by a wide velocity preferendum. Caution is required when comparing velocity measurements of a different type (i.e., mean station velocity, water column velocity, nose velocity) because the values are frequently not well correlated (Bovee 1986). Parr velocity selection may also be related to both the velocity of the holding position (nose velocity) as

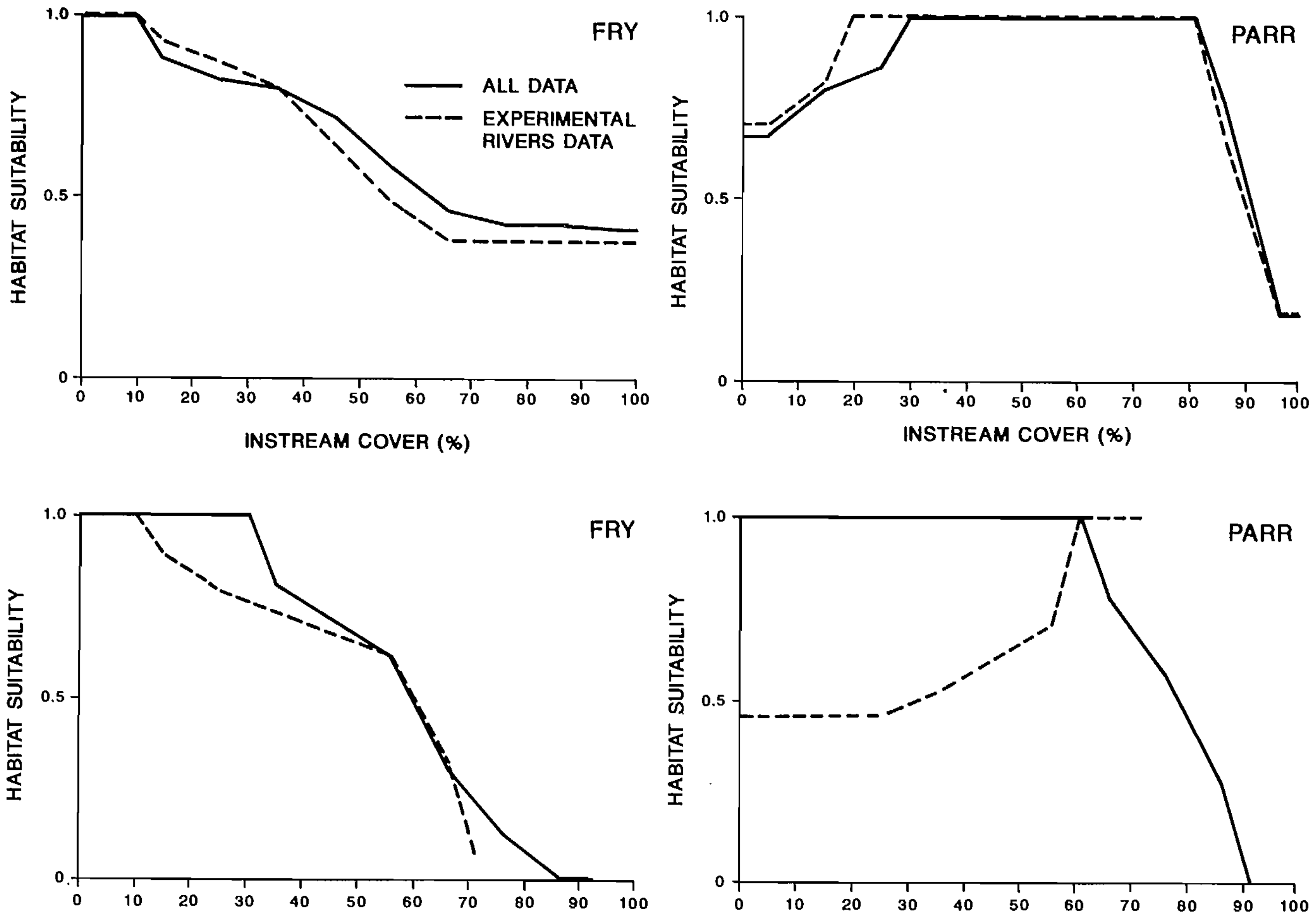

FIG. 4. Habitat suitability curves for Atlantic salmon fry and parr in relation to instream cover and overhanging cover.

well as that of the adjacent current (Wankowski and Thorpe 1979). Results in this paper suggest the measure of velocity employed (mean station velocity) in curve development may be a poor indicator of available holding sites with suitable flow conditions within a station. Other habitat attributes (e.g., cover, depth,), behaviour (e.g., height of holding position off of substrate) and biotic factors may obscure preference for a given velocity range (Gibson 1990). Refinement and evaluation of velocity curves presented in this paper are required before considering broader application.

Depth suitability curves presented in this paper are supported by observations reported in other studies (Egglishaw and Shackley 1982; Gibson and Power 1975; Symons and Heland 1978; Kennedy and Strange 1982, 1986). The consideration that, generally, salmon occupy faster, deeper water over coarser substrates as they grow has been well established (as reviewed by Gibson et al. 1990; Heggenes 1990) and substantiated in microhabitat research (deGraff and Bain 1986; Morantz et al. 1987). Depth selection, or conversely the availability of holding positions of suitable depth, is also more important in smaller streams than in larger streams and rivers (Heggenes 1990). Morantz et al. (1987), in New Brunswick and Nova Scotia rivers, found parr to select deeper waters than fry (optima from 30 to 60 cm as opposed to 20 to 40 cm for fry), and depths selected by both life stages were rarely less than 15 cm and did not exceed 100 cm. The high suitability associated with the greater depths for parr in this paper may be related to the ability of juveniles in Newfoundland to use deeper, slower water and pool habitats in the absence of competition from other species, similar to that reported by deGraff and Bain (1986). Kennedy and Strange (1982) have reported on the influence of interspecific competition from brown trout (*Salmo trutta*) on depth selection by salmon parr.

Suitability curves for ice scar (scour) height, a surrogate for range in discharge or 'flashiness', are also consistent with the previously mentioned relationships between stream order, stream morphometry (width, depth, gradient), runoff (discharge) and fish production (Vannote et al. 1980). The fry and parr curves (Fig. 3) demonstrate declining suitability with increasing hydrological instability. Small streams respond more rapidly to hydrological events than mainstems; however, the effect of peak flows and associated ice conditions is often more extreme in larger rivers (Horton 1945). Rivers (sites) with a high range in discharge are hydrologically less stable and may have low egg-to-fry survival due to substrate movement, washing out of redds, and unfavourable conditions for fry survival after emergence (Hynes 1970). Hydrologically unstable systems have poorly developed riparian vegetation and experience episodes of stream bank erosion and siltation often resulting in poor quality habitat conditions. The parr curve demonstrates higher suitability at the greater ice scar heights, than for fry, which could be reflective of coarser substrates associated with 'flashy' sites.

Substrate preference curves have been determined from an index weighted to increasing coarseness. Substrate particle size is related to water velocity, because greater flows are capable of transporting larger materials, as well as to discharge, volume, gradient, and geology (Amiro 1984; Platts 1979; Rimmer et al. 1984). The index employed in curve development cannot be related directly to dominance of any one substrate type, however, the rating curves suggest fry preference for pebble/cobble-dominated sites and parr for boulder-dominated stations. Morantz et al. (1987), in studies on Nova Scotian and New Brunswick rivers, found salmon to occupy faster water over larger substrates as they grew. Talbot (pers. comm.) found bottom type to influence parr densities on the Little Codroy River, Newfoundland, with highest densities associated with rough cobbled bottoms, large boulders and coarse rock. Gibson et al. (1990) have cautioned that apparent preference of parr for coarse substrates may be determined by other conditions (e.g., water velocity, territoriality, turbulence). Fry substrate preference may be related to association of fry with spawning habitats (gravel/pebble-dominated reaches) and that fry migration and displacement from spawning reaches is limited (Gibson et al. 1990).

The suitability curves for the two cover variables (instream and overhanging) provide results that are not as readily interpretable. Highest fry suitability was associated with low values for the cover variables with declining suitability as the percentages of these cover types increased. Conversely, Pickering et al. (1987) found salmon fry to have a high affinity for overhead (overhanging) cover. Gibson et al. (1990) found salmon biomass on the Experimental Rivers (southeast Avalon Peninsula) to have a negative relationship with overhanging cover. Trout in these rivers were most abundant in small streams in association with pool habitat and overhanging cover (Gibson et al. 1990). Increasing amounts of overhanging cover results in lower solar radiation inducing cooler temperatures that provide habitat conditions that may be better suited to trout (Binns and Eiserman 1979) or, alternatively, may be associated with headwater streams that migrating salmon may have difficulty accessing. The parr curve for instream cover is extremely flat and possibly is indicative that this attribute has little influence in habitat selection, relative to other variables. Gibson (1978) and Heggenes (1990) have reported salmon parr show a marked preference for turbulent water surfaces (as a type of overhead cover), however this factor cannot be considered in isolation of the increased water velocities that create this feature. Gibson and Power (1975) have reported that overhanging cover attracted parr in shallow water but not in deeper water. The influence of other variables on selection of cover, and the possible interaction with brook trout in this selection, should be examined in evaluating and refining the cover suitability curves.

The relative distributions of variables used in curve development is an important consideration when constructing and applying suitability criteria. Curves developed from a range of data should be limited in applicability to a comparable range in habitat attributes or very cautiously applied outside of that range (Bovee 1986; Bovee and Zuboy 1988). Data used in our paper were collected from electrofishing stations and the range in habitat attributes is constrained by limits imposed by the electrofishing methodology (i.e., wadable streams of moderate depth and flow). Suitability curves were developed from pooled data for a diverse set of rivers, and criteria could be considered to be representative of the range in habitat that juvenile salmon will use in relation to the variety of conditions to which they are exposed throughout the distribution represented in these data sets.

The distribution of the habitat variable used in developing suitability functions can influence the shape of the curve as well as the range of applicability of the curve. This influence is particularly evident in the suitability curves developed for width (Fig. 1), ice scar height (Fig. 3), and substrate rating (Fig. 3) where the narrower range in habitat variables for the EXP. RIV. data set has influenced the shape of the curves and constrains the applicable range of the suitability function. Small sample sizes or absence of data at the tails of distribution of habitat attribute data can give disproportionate weighting to values at these ranges. This effect was not a concern for variables used in suitability curve development, however other variables (e.g., pool attributes, Tables 2 and 3) had more irregular distribution which confounded attempts to define preferences using methods employed in this paper.

Ideally, for habitat suitability curves to have value for management of habitat, they should have wide applicability, since developing or defining suitability for each river and for each potential habitat perturbation are unrealistic. It can be argued that developing habitat suitability relationships from population level data for a stream reach or station will obscure the relationship between the microhabitat preferences and available habitat. It follows that suitability criteria developed from individual data will have limited application to habitat assessments of stream reaches/stations. Potential habitat perturbations are frequently evaluated in a general sense, not in a microhabitat context, and this level of prediction of impact may be better addressed from generalized suitability indices developed from population/station level data. A need exists for both levels of habitat suitability criteria, those that can be applied at an operation level as well as detailed (possibly site specific) suitability criteria for large-scale habitat assessments that require a greater degree of precision and confidence (e.g., Instream Flow Incremental Methodology studies).

Habitat suitability curves contain a host of assumptions and limitations that may constrain their potential application or increase the liabilities associated with their use (Bovee and Zuboy 1988). A major assumption in developing habitat suitability relationships for individual attributes is that of independence between the effects of variables. The interdependence of factors in habitat selection by juvenile Atlantic salmon is well-known and is related to complex interactions between several variables (reviewed in Gibson et al. 1990). The nature of the interdependence and possible compensatory mechanisms is not well understood. Developers of habitat suitability models have attempted to integrate the effects of individual variates (Terrell 1984; Trail and Stanley 1984; Gilbert 1984) while others have pursued the development of bivariate and multivariate suitability criteria (Hansen 1988; Voos and Lifton 1988; Lambert and Hansen 1989). Univariate and bivariate criteria may be particularly useful when a potential perturbation will affect only those variables. Other limitations of this approach include problems related to the transferability of curves between geographical regions, rivers and stream reaches, seasons and years, populations, and within the range in the habitat variables themselves (Lister 1988; Terrell 1984; Shirvell 1989). Suitability curves/models can be used to evaluate interactions between fish and their physical and chemical environment but do not consider biological factors, such as competition, behaviour, predation, or the effect of these influences on habitat selection (Bovee 1986). Development of suitability criteria is often a subjective process (Terrell 1985; Bovee 1986), however, subjectivity is important in allowing knowledgeable specialists to bring elements of their experience into the process, particularly when the approaches are adapted for use in a management context.

Conclusions

Habitat suitability curves developed in this paper, for station level data from a diverse set of rivers and habitats, should be considered as a set of macrohabitat level indices. These types of suitability criteria may be well suited to broad-scale habitat management needs and may be most useful as 'planning level' indices. For example, these suitability criteria define a set of stream characteristics that may warrant a high degree of protection from potential habitat perturbations. Suitability criteria developed at this level will have a wide range of applicability, while recognizing that river or reach-specific suitability functions may be preferred in situations where a high degree of precision and confidence is required.

Variables evaluated in this paper were collected to elucidate relationships between fish production and habitat attributes (Gibson 1990) and were not collected with the intention of developing habitat suitability criteria. Suitability criteria presented in this paper may require further refinement and testing over a wide range of habitat types and rivers before determining the full potential of application of the curves to management decisions. A more comprehensive and specific set of habitat evaluation criteria may be required to address the full range of potential habitat management applications. Additional parameters useful in evaluating potential habitat perturbations would include availability of pool habitat, % fines/degree of imbeddedness of substrate, and a suite of chemical and environmental parameters (water temperature, dissolved oxygen, nutrient content, turbidity and others). The effects of interspecific competition, primarily from brook trout (*Salvelinus fontinalis*) in insular Newfoundland, on habitat selection and the shape and trend of suitability curves should be investigated. Standing waters contribute significantly to salmon parr rearing and potential production (Pepper et al. 1985) in insular Newfoundland and this fact would need to be recognized in the development of habitat suitability indices/models to be applied in this geographical area. Separate HSIs would need to be developed for different habitats (i.e., for lacustrine and riverine habitats) or conversely a model would need to consider habitat requirements/use of the various life stages in both lentic and lotic habitats. Curves developed in this paper need to be cautiously applied to other geographical regions where interspecific competition will influence habitat selection.

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Estimating Production, Food Supplies and Consumption by Juvenile Atlantic Salmon (*Salmo salar*)

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POWER, G. 1993. Estimating production, food supplies and consumption by juvenile Atlantic salmon (*Salmo salar*), p. 163–174. *In* R. J. Gibson and R. E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

Methods of estimating biomass and production of stream salmonids are reviewed. The few measures of production of juvenile Atlantic salmon make it difficult to evaluate controlling factors over the range of habitats occupied by this species. Only general descriptions of diet of wild fish are available. Estimating benthic production is thwart with problems of sampling and species diversity, as well as debate over methodology. In field experiments, it has generally not been possible to show that fish in stony streams can reduce the abundance or alter the composition of the benthos. A physiological approach should be used to evaluate energy needs of Atlantic salmon parr in relation to temperature, growth, competition and the food required to support production. Direct or remote observation could be used to study feeding rates food selection and ration.

Nous examinons les méthodes utilisées pour estimer la biomasse et la production de salmonidés dans les cours d'eau. La rareté des mesures de la production du saumon atlantique juvénile rend difficile l'évaluation des facteurs agissant dans l'ensemble des habitats occupés par cette espèce. Nous ne disposons que de descriptions générales du régime alimentaire des poissons sauvages. L'estimation de la production benthique est freinée par des problèmes d'échantillonnage et de diversité des espèces, ainsi que par le débat sur la méthodologie. Dans les expériences de terrain, on n'a généralement pas pu montrer que la présence des poissons dans des cours d'eau à fond rocheux peut réduire l'abondance ou modifier la composition du benthos. Il faudrait avoir recours à une approche physiologique pour évaluer les besoins énergétiques des tacons de saumon atlantique en fonction de la température, de la croissance, de la concurrence et de la nourriture nécessaire pour soutenir la production. On pourrait se servir de l'observation directe ou à distance pour étudier le taux d'alimentation, le choix des aliments et la ration.

Introduction

An evaluation of the trophic pathways supporting the production of juvenile Atlantic salmon (j.A.s.) is very difficult to achieve, but worth attempting. By enabling us to understand the functional relationships with the salmon's habitat, it provides clues as to how these may be enhanced or constrained by human actions. Production (P) is the product of instantaneous growth rate (G) and mean biomass (B). For accuracy, the intervals between measurements should be short and annual production summed over the year. Chapman (1978) provides a full discussion.

Relating riverine fish production to the productive capacity of the habitat may not be an easy task. A direct link between lotic secondary production and the biomass of j.A.s. in any habitat, although generally acknowledged, has never been established. This is probably because only a proportion of the potential food in any habitat is consumed by salmon parr and the food may be produced *in situ* or elsewhere. The diet of j.A.s. changes with habitat and season and includes a variable contribution from terrestrial habitats. The aquatic food webs, likewise, include allochthonous inputs. Mann (1969), in attempting to review the workings of aquatic ecosystems, concluded they were probably too complex to analyze in full detail and that we would probably have to be satisfied with broad, general outlines.

The many nuances and foundations of our methods of studying fish were reviewed by Magnuson (1991). He emphasized the diversity of disciplines that have contributed to the emergence of modern fisheries ecology. However, for any particular species, the contributions are uneven. The very value of Atlantic salmon has influenced the way we study it. It has affected the kinds of questions asked and the types of data gathered.

Most current research is concerned with the practical aspects of aquaculture, including nutrition, genetics, control of parasites and disease. Wild stocks have received less attention, except where problems have been perceived such as acid precipitation, industrial pollution, over fishing and habitat loss. Work has been focused on the autecology of the species, rather than on the entire ecosystem, including the food webs, and the community of organisms that share its habitat. As rivers and streams are degraded, runs depleted by fishing and gene pools contaminated by escapees from aquaculture, wild stocks become even more valuable. The traditional method of getting data on diet and food consumption of wild fish is not acceptable since it involves killing too many fish. Biomass estimates of j.A.s also present problems since handling and weighing inevitably causes stress to fish as well as risk of damage and mortality. If we are to relate the biomass of j.A.s. to the productive capacity of their habitat, new approaches need to be considered.

My aim in this paper is to review methods that have been used to estimate stream salmonid production and the biomass and consumption of prey supporting this production. Because of the limitations of the methodology, it is unlikely that firm relationships can be found between trophic levels in the food webs supporting j.A.s. Instead, it might be more useful to estimate energy requirements in the laboratory using methods that have been employed for other salmonids. This, combined with direct observations on feeding rates, food selection and energy contents of prey, should provide the data required to estimate energy flux through j.A.s. and can be done without sacrificing wild fish.

Estimating Juvenile Atlantic Salmon Biomass

Estimating biomass is essentially a numbers game. Since it is never possible to count all fish in a river, sampling is required. The choice of sampling areas depends on access, time and manpower available and the suitability of sites for application of the chosen method. Every method involves assumptions which should be met to satisfy the statistical requirements of the calculations. The assumptions are not always testable and the experience of the operators is resorted to to judge the validity of data. Once numbers have been obtained, weights are easily measured, although it should be recognized that weighing live, anaesthetized fish, in the field, involves some error. To avoid stressing fish, weights may be estimated from a previously developed length-weight relationship (Egglishaw and Shackley 1980).

Estimates of numbers of j.A.s. followed earlier work on marking marine fish to track migrations, measure rates of exploitation and census stocks (Ricker 1975). Information on the abundance of salmon parr was required for several reasons: to try to relate abundance to the productivity of the habitat; measuring the impacts of spray programs to control forest insect pests (Elson 1967); estimation of optimal stocking densities to maximize smolt output (Elson 1957a, 1957b, 1975); and to examine the role of avian predators (Elson 1962). More recently, the pace of work on this topic has accelerated in concert with our perception of danger to the resource due to declining stocks.

A variety of methods have been used to determine the abundance of salmonids in streams. Early estimates used seines, trap nets and hand trawls (Allen 1944, 1951) and these methods are still sometimes used (Elson 1962; Gibson 1973; Ryan 1990).

In the 1950's and 1960's, rotenone became available in emulsified form and was suitable for sampling small streams. It can be oxidized with potassium permanganate and used to sample sections of streams or branches around gravel bars and islands in larger streams (Power 1973). Its major drawback was that it killed fish and, for that reason alone, it would not be used today. A light at night was used to count and estimate production of brook char in small streams by O'Connor and Power (1976). This technique can only be used in small streams where it is possible to wade or walk along the banks. Allen (1951) used a light for some of his sampling in the Horokiwi and Power and Shooner (1966) collected salmon parr this way in the Nabisipi River when other methods failed. It has never been tried to quantitatively sample j.A.s. but it would be possible in some streams.

Electro fishing is unquestionably the preferred method in the places where it can be used. The increased efficiency and built in safety features of modern machines, together with the fact that induced electronarcosis does not harm the fish, are the advantages. Randall (1990) has thoroughly reviewed the practice as it is applied to estimating abundance of salmon parr in eastern Canada. The removal method, or Zippin's method, based on multiple passes through a net enclosed survey area and a capture probability generally between 0.3 and 0.6 gives good precision. This method may be combined with a Peterson estimate if fish are marked and released on the first pass. According to Randall (1990), both methods give similar precision if 3 or more passes are made. Biases may be introduced if fish are disturbed while installing enclosure nets, if fish of different sizes have different probabilities of capture, or for the Peterson estimate, if marked fish are those most likely to be caught and recaptured or if marking affects catchability. Similarly, site selection may bias results because of distance from spawning areas, gradient, depth, substrate or intra-specific interactions between age classes affecting proportions (Gray et al. 1989). Site biases are particularly difficult when the aim is to estimate numbers of young salmon in an entire tributary or river. Juvenile salmon are contagiously distributed along the length of a river and variances of estimates at sample sites exceed means. Randall (1990) discussed the problem of choice, size and distribution of sampling sites. He also recognized that, in large rivers where it is not considered possible to determine absolute abundance, an index of relative abundance can be used to detect trends in abundance. Fixed stations (>80) were used in the Miramichi in the early 1970's but now only 15 are monitored. Results from these 15 were significantly correlated with the higher number of stations and were providing a similar index (Randall 1990). Choice of a limited number of sites is risky because it is not possible to monitor events in all available habitat-types nor in a large number of tributaries. If total numbers vary with area occupied, which may depend on water conditions during migration and spawning in previous years (Power 1981; Gibson et al. 1987), downstream sites may not detect changes in stock abundance.

The Schnabel, or multiple mark-recapture method, recommended by Seber (1986) has advantages in some situations. It allows testing assumptions of equal probabilities of capture, however, it necessitates more handling and effort. It was used effectively by Ryan (1990) to census brook trout and Atlantic salmon abundance in two headwater lakes of the Gander River, Newfoundland. The validity of the census results (20 and 24 estimates, both species, 2 lakes) were checked by comparisons of frequencies of marked fish in the population on the penultimate sampling days with frequencies in the final census samples; by the relationships between catch per unit effort and population estimates, and by comparing age distributions and numbers of migrating smolts with smolt ages of returning fish and angler success. Estimates were considered reliable and the method provided a practical way of monitoring the stocks. Dempson and Stansbury (1991) used partial counting fences and a two-sample stratified design for estimating smolt numbers in a large Newfoundland River, confidence limits were <8% of the estimate.

Since a high proportion of salmon habitat is remote and inaccessible, there has been considerable effort put into finding proxies for salmon abundance. The use of air photographs to inventory salmon habitat was suggested by Dubois and Clavet (1977) and the technique was refined and applied to a range of physio-graphic conditions in Quebec by Clavet (1980). It was used by Belzile et al. (1982) in the Delay River, a major salmon producing tributary of the Koksoak River in northern Quebec. Three categories of habitat were recognized on the basis of depth, velocity and substrate. Salmon abundance was estimated by divers counting numbers and recording sizes of parr along transects in each habitat category. From counts and areas, total numbers were estimated. The 95% confidence intervals were based on the fit of counts to a Poisson distribution. The methodology as it is currently used in Quebec was reviewed by Côté et al. (1987) and discussed further by Tremblay et al. (1993) and Caron and Talbot (1992). The technique is being evaluated for estimating the total parr population in the Trinity River (Caron and Ouellet 1987). An obvious benefit of the methodology is that it can be used to evaluate the capacity of habitats to support salmon where they are now absent. An equally obvious drawback is that it is insensitive to changes in abundance since it assumes stocks are at carrying capacity. Amiro (1983, 1984) used air photographs and stream gradients to measure area and quality of j.A.s. habitat in New Brunswick and Nova Scotia.

Caution must always be used in interpreting the results of estimates of abundance. Where attempts have been made to check the accuracy of estimates, considerable errors have been identified, even when conditions governing the estimate seemed ideal. Mahon (1980) compared electrofishing estimates with total populations using rotenone to catch "missed" fish. For a variety of species of stream fish from five Polish and six Canadian locations, electrofishing underestimated numbers by 20%. Errors were related to location, type of gear, and species differences, with small benthic species often greatly underestimated.

Production Studies

Confusion arises in the literature on production of stream salmonids because the word production has been used with quite different meanings. Here it is always used to mean biological production (P) which, for anadromous Atlantic salmon, is the more restricted usage. Smolt production (output), meaning the annual numbers of smolt leaving a system, is the commonest usage. It is also used in the industrial sense in reference to the products of aquaculture or fisheries. There are considerably more publications concerning smolt output and the factors that control it than with production. Examples include the effects of predator control (Elson 1962; Heggenes and Borgstrøm 1988; Anderson 1986), of forest spraying (Elson 1967), of industrial activity (Elson 1974), of fisheries (Paloheimo and Elson 1974), and, most recently, acidification (Watt et al. 1983).

Most studies of production and population dynamics of stream salmonids have dealt with species other than Atlantic salmon. Excellent examples include the brook trout (*Salvelinus fontinalis*) of Lawrence Creek, Wisconsin (Hunt 1966, 1971 and 1974) and the anadromous brown trout (*Salmo trutta*) of Black Brows Beck in the English Lake District (Elliott 1984a, 1984b and 1993). The Lawrence Creek work, conducted over 11 years, showed that production by the population was relatively stable and regulated through compensatory adjustments in growth and mortality rates among age groups. In one section of the creek the habitat was improved and this increased production, but, in other sections, production declined, showing that over short distances there was more interconnection between sections than suspected. Yield to anglers was only a small proportion of the fish biomass elaborated.

Elliott's publications describe one of the most comprehensive studies of a trout population ever undertaken. There was a large variation between year-classes in egg deposition, high survival to emergence, but subsequent mortalities were density-dependent. The number of recruits in May–early June was related to the egg deposition by a Ricker, dome-shaped, stock and recruitment curve. The curve was considerably flattened by August-September. Mortality rates were highest in the period after emergence when the young fish were attempting to establish feeding territories and declined during the summer. Losses to the population were believed to be due to mortalities rather than dispersal. Physical factors, water velocity and temperature, exerted no discernable effect on trout numbers, although temperature clearly affected development rates. Black Brows Beck, however, has a stable bed and does not experience high water velocities because, during flooding, it overflows the normal channel. Temperatures were also moderate and unlikely to stress the trout.

Intrinsic factors, perhaps relating to food and space, appeared to operate to regulate numbers of fish at different stages of the life cycle to the carrying capacity of the habitat. The mechanisms were not easy to discern. The size of 0+ trout at any time could be estimated with reasonable accuracy from the initial size and temperature regime, assuming maximum rations and using the growth model developed by Elliott (1975). Except during three dry years, food did not appear to be limiting. Individual variation in size of 0+ trout was low at emergence (C.V. 7.5%, length; 14%, weight) and increased rapidly during the first month and then stabilized in a manner that was inversely related to initial density. Biomass estimates ranged from 0.90 g m^{-2} to 3.89 g m^{-2} in May–early June and from 1.21 g m^{-2} to 7.36 g m^{-2} in August–early September and were predominantly influenced by numbers of fish. A Ricker curve described the relationship between production and the density of eggs or alevins at the start of each year class. Egg deposition explained most of the inter annual variation in production. Investigations in Black Brows Beck produced no evidence for density-dependent growth, only evidence that, as densities increased, there was more conformity in size. Temperature remained as an important environmental variable, as did factors external to the nursery stream that affected the size, condition and numbers of spawning trout.

These studies suggest that production is relatively stable, even though the elements contributing to it are more variable, and that mechanisms exist within species to adjust production to an appropriate level for the environment. In judging this work it should be remembered that it was carried out in small, relatively stable, streams. In contrast, Atlantic salmon occupy a variety of habitats, from gentle streams to harsh glacial fed rivers. Stocks are heavily exploited and this has affected egg deposition so that many stocks are now believed to be well below historical levels.

There have been few investigations dealing with the production of j.A.s. (Table 1). Production estimates range from almost zero to over 1 kg·100 m^{-2}·yr^{-1}. Higher values generally occur in the richer European streams (Gibson and Myers 1986) and lowest values in the glacier fed streams of north Norway (Power 1973).

The results of these investigations are difficult to compare because different authors have used a variety of sampling methods and intervals between measurements vary from weeks to a year. Even when the same sampling method has been used, its accuracy and representativeness in streams of different size and character is not known. The values are also influenced by the mix of species in the communities

TABLE 1. Estimates of annual production of Atlantic salmon parr.

Author(s) Year	Reference	Location	Production g 100 m² yr⁻¹ (mean)	Comments
Randall, R.G. and M.P. Chadwick 1986	Pol. Arch. Hydrobiol 33: 391–409	Miramichi	67.9–161.2 (130.0)	below carrying capacity
		Restigouche 1972–1983	38.2–90.0 (60.0)	below carrying capacity
Egglishaw, H.J. and P.E. Shackley 1977	J. Fish Biol. 11: 647–672	Shelligan Burn 1966–1975	549–1212 (894)	Range based on one section (min) or two sections (max)
Randall, R.G. and U. Paim 1982	Can. J. Zool. 60: 1647–1649	Mirimichi 3rd order tributaries 1976–1978	27.4–512.3	below carrying capacity
Gee, A.S. et al. 1978	J. Fish Biol. 13: 439–451	Wye River 1975–1976	30–110	
Power, G. 1973	Rep. Inst. Freshw. Res. Drottningholm 53: 78–111	Komag, Storelva, Russelva, Leirskarelva 1963, 1966	1–133 (50.5)	Range and mean of 22 sites with salmon
Chadwick, E.M.P. and J.M. Green 1985	Verh. Internat. Verein. Limnol. 22: 2509–2515	Western Arm Brook 1972–1977	160–290 (223)	Fluvial habitat adjustment for 73% efficiency of sampling. Probably underestimated
Randall, R.G. et al. 1989.	Proc. Nova Scotia Inst. Sci.	2nd order tributary, Philip 1968–1988	203–261 (232)	*Salmo trutta* production about equal
Gibson, R.J. and R.A. Myers 1986	Proc. 17th Ann. Study Course, Inst. Fish. Mgt.	Highlands	62–164 (115)	*S. fontinalis* production varies with site (38–389 g 100 m² yr⁻¹) if present

studied; the effect of this is hard to evaluate. Total salmonid production may be increased in the presence of *Salmo trutta* or *Salvelinus fontinalis* but Atlantic salmon production is almost certainly depressed. Quantitative measurements involving experimental manipulations of community structures are the only real way to test the effects of species interactions and these present considerable experimental difficulties in the field.

Transplanting anadromous salmon into zones above barriers to upstream migration, as was done by Gibson and Dickson (1984), is one experimental approach, another is removal of potential competitors as recommended by Fausch (1988). Results may be hard to interpret, being confounded by advantages resident fish may have over those introduced, by absence of other fish and planting densities (Heggenes and Borgstrøm 1991), by disturbance and changes in density as a result of removal.

Factors that affect production of j.A.s. comprise those that control growth rate and population density. These include the array of abiotic and biotic factors that constitute the aquatic habitat and those influencing the surrounding catchment. The terrestrial habitat must be considered, since much of the energy and material flux through the stream ecosystem is allochthonous. Added to these factors is the rate of egg deposition which determines the starting point and sets the level of production (Randall and Chadwick 1986).

Egglishaw and Shackley (1985), reviewing the factors controlling the production of juvenile salmon in Scottish streams, identified a number of physical, geological and biotic factors as being important. Temperature determined the date of emergence of fry, the duration of the growing season and the growth increment. Intra-specific competition had an effect on the sizes of 0+ fish which were negatively correlated with density. They also presented some evidence of competition between year classes. Data on interspecific competition with trout came from estimates of survival rates of salmon fry which were higher in the Tummel Valley, where trout densities were lower than elsewhere. Territories occupied by juvenile salmon in streams were regulated by depth. Therefore, discharge could influence densities at particular sites and, perhaps, overall stock. Water conductivity and salmon biomass were correlated, with best production in streams in sandstone areas or associated with limestone outcrops. They concluded that data on causes and rates of mortality, especially the roles of predation, disease and other factors, were needed to improve management of salmon in Scotland.

The stability of the stream bed, width of channel, characteristics of the surrounding valley, turbidity and length of growing season were suggested as factors determining the levels of production in north Norwegian rivers (Power 1973). Winter conditions, particularly the amount of suitable winter habitat, are likely to control densities and levels of production in northern rivers (Cunjak 1988; Cunjak and Randall 1993). At the southern extreme of the range, the extent of cool groundwater sources, tributaries and headwaters is likely to limit production. Gibson and Myers (1986), in reviewing production of j.A.s., concluded North American rivers were more food limited and more constrained by temperature and discharge than most European rivers. A single explanation seems insufficient to describe control of production in the range of habitats occupied by j.A.s.

Estimating production requires considerable effort and expense and its accuracy depends on a number of assumptions beyond those that must be met for adequate sampling of biomass. All assumptions relating to estimating growth rate from measurements of fish (weight, length) at intervals must be met. In particular, there should be no bias due to size related differential mortality. When intervals between measurements extend over long periods, like winter, and fish are subject to considerable density-dependent mortality, it is not certain that this assumption is justified. Calculations of production involve assumptions concerning the patterns of mortality and growth between intervals which are adequately discussed in reviews of the methodology (see, for example, Chapman 1978) as well as assumptions relating to sampling. Another problem is the question of mobility. Almost all studies assume that fish do not move much during the summer growing period, when most production occurs, and evidence from both tagging and counting fence data supports this. But movement is a relative term. As fish grow they select water of faster velocity (Morantz et al. 1987; Rimmer et al. 1984) and this would generally be associated with greater depths. The assumption that survivors of the same group of fish are being sampled at the same site in successive intervals may be true for small, low order, streams but it is less likely to be true for sample sites in large rivers. The mobility of the fish must be greater at sites in big rivers, not only because as fish grow they have more choice of locations, but also because water levels and velocities fluctuate more. There are also movements associated with temperature at low flows as fish seek refuge in pools and near groundwater sources (Saunders and Gee 1964). In addition, there are well documented movements in the autumn as mature male parr move upstream and others seek winter habitat (Rimmer et al. 1984; Cunjak 1988). Index sites in large rivers may provide biased samples because only shallow sites can be sampled using electrofishing gear while other bias may occur because of interactions between year-classes (Gray et al. 1989).

Other factors that are more pervasive must also be considered. An example is acid precipitation, but there are other widespread toxic materials entering aquatic ecosystems as well as more localized sources of pollution that can impact production. In Nova Scotia, water chemistry and pH were examined for effects on salmon production by Lacroix (1989). At a pH 4.9 in Westfield River, production was < 40 g·100 m^{-2}·yr^{-1}, while in the neighbouring North River, at a pH 5.9, it was 140 g·100 m^{-2}·yr^{-1}. The contrast was due to differences in density rather than growth. Production in the North River was not greatly depressed compared with values in Table 1. Densities in the Westfield River were not reduced because of low egg deposition, but because of high mortality of post-emergent fry. This was attributed to low pH rather than aluminium which was present in a non-toxic organic form in these rivers.

The Diet of Juvenile Atlantic Salmon

Allen (1941) justified detailed studies of j.A.s. diets in order to establish relationships between the benthos and the prey species consumed. These could be used to assess the food value of the benthos and predict diets in habitats where the benthos was known. This objective has not been realized. One reason is that j.A.s. are such a valued resource it is not acceptable to kill them in sufficient numbers to provide information on diel changes in stomach content, seasonal variations in diet, prey preferences as related to age or size, or estimate daily ration in the wild.

Data that are available provide good general descriptions of the diet, indications of the quantities of food likely to be present in the stomach during the day, and information on seasonal and geographic variation in prey. Some sources of dietary information are listed in Table 2, together with the kind of data available. In general, the diet of j.A.s. varies with location, size and season. Salmon parr, like most temperate region freshwater fishes, are opportunistic feeders (Larkin 1956; Hunt 1975), consuming the most easily available, appropriately sized, prey that their habitat provides. Late summer, when most aquatic insects have emerged and oviposited, seems to be a season of reduced food availability and consumption. Many salmonids compensate for the lack of aquatic food by switching to terrestrial invertebrates at this time. Hunt (1975) reported numerous examples in which a high proportion of the diet and energy was provided by surface drift. Atlantic salmon parr appeared to be less dependent on allochthonous food than some salmonids, perhaps because, in their preferred riffle habitat, surface turbulence renders such prey less visible.

The late summer decline in stomach content might also be caused by including fish in the samples which would not smoltify next spring. These fish belong in the lower modal group (LMG) which, under experimental conditions, are less likely to intercept, and, if they attack, are less likely to consume a food particle at this time (Metcalfe et al. 1986). Food intake is reduced and the fish behave so as to minimize the cost of obtaining a maintenance ration. The parr destined to become smolts next spring (UMG) continue to feed actively. When threatened by a predator, they exhibit a smaller reduction in feeding intensity than LMG parr, although the absolute reduction in food consumption is the same for all threatened fish (Huntingford et al. 1988a). In August, UMG parr selected areas of faster flow, with more food, but

TABLE 2. A selection of publications giving information on the diet of Atlantic salmon parr.

Author(s) Year	Reference	Location	Information
Allen, K.R. 1941	J. Anim. Ecol. 10: 47–76	Eden, England Thurso, Scotland	Numbers, dry weights, prey, annual variations, composition of benthos, selection
Baglinière, J.-L. 1980	Cybium 9: 81–90	Elle, France	Smolts, annual variation, numbers and percentage, composition of prey
Egglishaw, H.J. 1967	Freshwat. Salm. Fish. Res. 38: 1–32	Shelligan, Scotland Almond, Scotland	Numbers, dry weights, prey, annual, composition of benthos, variability in diet
Gibson, R.J. and R.A. Cunjak 1986	Can. Tech. Rep. Fish. Aquat. Sci. 1472: 82 p.	Salmonier, Newfoundland Broad Cove, Newfoundland	Diet overlap, selectivity indices, 4 groups of prey
Power, G. 1969	Arctic Tech. Paper 22: 72 p.	Koksoak, N. Quebec George, N. Quebec Whale, N. Quebec	Percentage composition, volume, occurrence, summer
G. Power and G. Shooner 1966	J. Fish. Res. Board Can. 23: 947–961	Nabissipi, Gulf of St. Lawrence, Canada	Frequency occurrence, volume, July August, Estuary, River
Thomas, J.D. 1962	J. Anim. Ecol. 31: 175–205	Teify, Wales	Occurrence, points, annual, composition of benthos
White, H.C. 1936	J. Biol. Board Can. 2: 499–506	Apple, Nova Scotia, Canada	Dominant foods, volumes June–September

greater risk of predation and were less likely to abandon their station when threatened by a predator than LMG fish (Huntingford et al. 1988b).

Benthic Invertebrate Production

Secondary production is generally taken to mean all invertebrate production, including herbivores (Downing and Rigler 1984). Its study is important for elucidation of energy and material transfers within communities and ecosystems. From such information, general theories of trophic-dynamic relations can be developed which allow predictions and identification of limits. Management can then be concentrated on changing those factors which promise to provide the most benefit (Downing 1984).

Methods of measuring invertebrate production are described in Downing and Rigler (1984). There is still intense debate on the accuracy of the different methods (Plante and Downing 1990; Iverson and Dall 1989). Complexities arise because of the varying lengths of life cycle, rates of development, and overlapping generations among invertebrates. Questions concern the use of average life spans for communities or whether species have to be treated separately. Much of the debate revolves around levels of accuracy required which depends on the purpose for which the data is intended. Because of the amount of work required to estimate production, studies are usually restricted to one trophic level and habitat.

Peckarsky (1984, and references therein) reviewed the methods of sampling stream benthos and commented no progress had been made in the last decade to replace error ridden techniques. Surber or box samplers are unreliable to estimate biomass, production, or diversity. Because of contagious distribution of stream insects, many samples are required for reliable estimates, yet numbers of samples are often dictated by convenience or justified to avoid habitat destruction. Artificial substrate samplers have disadvantages, including risks of biased data and erroneous estimates of production. Core samplers established the importance of the hyporheic zone, overlooked by other methods, but can only be used in certain substrates and have their own problems. Peckarsky concluded that obtaining good estimates of benthic biomass or production in streams was impractical. Adding to the difficulties, Resh (1979) pointed out the need to take into account life history information and use appropriate techniques to sample different life history stages of each species.

Given this background, estimating the production of all invertebrate species contributing to the diet of j.A.s. does not seem feasible, nor, to my knowledge, has it been tried.

A number of attempts have been made to show the effects of fish on the benthic invertebrate communities of streams but they have met with little success. Allan (1982) reduced the density of *S. fontinalis* by 75–90% during four years in a section of an infertile Colorado stream. Although the trout grazed heavily on a few taxa, reduction of the trout had no demonstrable effect on either the benthos or the drift. Variability in invertebrate abundance makes it difficult to detect effects. Reasons for failure to see a change in prey abundance include the possibilities that trout consume only a small fraction of potential prey and that prey are adapted to the presence of predators and can avoid serious losses. Reice and Edwards (1986) confined predators (the salamander *Eurycea bislineata*, brook trout, and threespine stickleback) in cages with substrate and prey in two small Quebec streams. The experiments showed no significant effects on species richness, diversity or total numbers. However, in August, trout did reduce the abundance of most taxa. Brook trout did not appear to structure the macro-invertebrate communities of small streams. Using a similar approach, with *Semotilus atromaculatus,* Gilliam et al. (1989) concluded that the minnow could reduce invertebrate numbers. Oligochaetes and isopods were most affected and their sizes were reduced by size-selective predation.

The effects of fish on their food sources depend on the abundance and appetite of the predator and the abundance and availability of the prey. The latter is particularly difficult to measure for benthic invertebrates. The availability is more obvious when invertebrates enter the drift. Brittain and Eikeland (1988) reviewed the literature on drift and most of the prey of stream salmonids are important components of the drift in temperate streams. Drift increases at dusk and, to a lesser extent, at dawn, the diel pattern varying with the species and life history stage. This partly coincides with the diel pattern of feeding in j.A.s. reported by Hoar (1942). Drift distances vary with current, size of river, species and life history stage. Predators can modify drift patterns, indicating adaptive responses to avoid predation. Drift allows downstream redistribution of invertebrates but must be balanced by nymph and larval rheotaxis and upstream movement of imagoes. Fecundity of drifters is high and species can sustain considerable losses to predators or outstream migration. The numbers drifting at any instant are only a fraction of the benthos (0.004–0.130%) but a higher proportion (2.6%) changes position each day.

Thorp (1986), in reviewing the roles of predators in freshwater, made a number of important points. Some disagreements over the importance of predators are attributable to differences in the use of terms, others to a failure to distinguish between causes and maintenance of community structure. Field experiments, at best, can show local temporary depressions in prey abundance; none demonstrate these are more than temporary and are followed through to subsequent generations. Logic dictates that predators must reduce the abundance of their prey. At the same time, it is equally obvious that prey species cannot have their survival threatened. Prey and predators have co-evolved and are in positions of competitive balance.

These allow for fluctuations in abundance, but they are not sufficient to cause extinction. The dynamics of the interaction between stream fish and their food, combined with the problems associated with quantitative sampling of stream benthos (and other food sources) is the reason researchers have failed to show stream fish production is controlled by the food supply.

Discussion

The justification for measuring production of j.A.s. is to evaluate energy flux through the trophic level it occupies. Difficulties arise because diets do not place it at a particular trophic level. The food is obtained through the detritivore and herbivore food chains, through invertebrate predators and from various terrestrial food webs. No one has attempted to measure the energy flux through j.A.s. or relate production to the production of its main food items.

Rather little progress has been made with other stream salmonids to relate production of fish to that of the food base. In Valley Creek, Minnesota, Waters (1982) reported that annual production by *Salvelinus fontinalis* was closely correlated with production of its main prey, *Gammarus pseudolimnaeus*. During a 5-yr study, prey production was reduced by siltation and fish production declined in a similar pattern.

Annual energy flux through the trout population of Bisballe Bæk, a small Danish stream, was estimated using Winberg's balanced equation, with new values for assimilation efficiency, oxy-calorific equivalent and constants in the metabolism weight equation (Mortensen 1985). Equations and constants generated by Elliott provided a second method of estimating food consumption (Mortensen 1985). These methods produced different estimates of annual food consumption which, when converted to growth efficiencies by year class, ranged from 9.0 to 20.4%. For the entire population, estimates of gross growth efficiencies were closer, range 10.8 to 18.6%. Estimates of fish numbers were considered to be least accurate and confidence limits on these were applied to food consumption estimates. Elliott's equations were believed to provide the most reliable estimates of energy requirements. In 1974–75, trout production was equivalent to 88.9 kJ m^{-2} from consumption of 479.2 kJ m^{-2} food and in 1975–76 it was 65.8 kJ m^{-2} from consumption of 369.8 kJ m^{-2} food. Estimated production of herbivore and detritivore benthos was equivalent to 447.3 kJ m^{-2} and of carnivore species 23.0 kJ m^{-2}, which matches rather closely the estimated energy of consumed food.

Production studies do not hold much promise for the construction of energy flux models through trophic pathways leading to j.A.s. It is also doubtful whether the tremendous effort required to obtain the data needed to construct such models is justified. Since stream ecosystems are dynamic, densities and community structures change with time and measurements need to be repeated many times before the full range of possibilities can be seen. I agree with Chadwick's (1985) arguments for the need to establish monitoring programs on small index rivers. These are essential for providing early warning of potential problems and base-line data needed to understand large scale phenomena. Their role in understanding the effects of climate change is enough to justify the costs of the monitoring. If we are to develop useful predictive models of the dynamics of salmon stocks, the data provided by index rivers is required to develop and validate the models. Until this has been done, there are other approaches that should be considered to improve our understanding of the processes supporting j.A.s. These may have been overlooked because most biologists working on wild j.A.s. are field oriented and science is biased towards innovation.

Brett and his colleagues carried out some very elegant studies of Pacific salmon which combined laboratory measurements with field observations. The investigations into the growth of fingerling sockeye salmon (*Oncorhynchus nerka*) (Brett et al. 1969) are examples that should be followed for Atlantic salmon. If this was done, it would be possible to estimate ration from a record of growth rate in the field, which is relatively easy to acquire, and temperature. When applied to chinook in the Nechako River, British Columbia, fish were consuming about 60% of the maximum ration (Brett et al. 1982). Elliott (1972, 1975, 1976, 1984a, 1984b), in his work on brown trout, has also clearly demonstrated the advantages of combining experimental measurements on confined fish with field observations. His equations were used by Mortensen (1985) to estimate energy flux through a Danish trout population. An advantage of laboratory measurements is that fish are not generally killed, as they often are during field sampling, an important consideration when working on a species as valuable as Atlantic salmon.

Li and Brocksen (1977) adopted a physiological –behavioral approach to investigating the energetic costs of density-dependent activities (competition) by rainbow trout (*O. mykiss*) in a laboratory stream. They argued that energy consumed can be partitioned between growth and routine metabolism after subtracting the fraction not assimilated. Similarly, routine metabolism can be separated into a temperature dependent component for standard metabolism plus the sum of energy expended in various activities. Growth trials using isolated trout established that under experimental conditions space did not affect the responses to five levels of daily ration. In groups, growth rates, conversion efficiencies and fat contents of fish declined as population density increased. At higher population densities, variability between fish increased depending on whether fish were dominants or subordinates and this was attributed to the costs of social interactions. At highest densities, dominant fish did not always do best, expending time and energy maintaining their status, thus sacrificing some of the benefits. Trout at the bottom of the social hierarchy hid, avoided social contacts and would not eat. In nature and over longer periods, social status of fish would change as flows fluctuated and the values of territories changed. Subordinate fish would either die or move to another area. This approach to studies of competition should be applied to Atlantic salmon, not only for intraspecific competition, but also for interspecific competition. It has the advantage that the cost of interaction can be measured in energetic units. It runs the risk that results obtained under artificial conditions do not accurately reflect natural conditions.

The lack of information about the thermal relations of j.A.s. was remarked upon by Elliott (1991) when he presented a thermal tolerance polygon for juvenile Atlantic salmon. This species was the eighth in a list of salmonids for which this information has been obtained. Although construction of a thermal tolerance polygon requires many precise measurements following periods of acclimatization to a range of temperatures, the information has application to the environment. The upper limit for feeding was 22.5°C and fish fed at temperatures as low as 3.8°C. The upper incipient lethal temperature was 27.8°C, although salmon can tolerate temperatures higher than this for short periods. The use of this information in predicting the distribution of salmonids and the effects of climate change were discussed by Power (1990).

Other measurements that have been surprisingly lacking for j.A.s. are those concerning oxygen consumption. The methodology and instrumentation for measuring standard (basal) routine and active metabolism are well known (see Beamish 1978, for a review). Power (1959) attempted to measure basal oxygen consumption in the field, looking for evidence of adaptation to low temperature in northern stocks. Higgins (1985) measured oxygen consumption and presented equations relating resting rates to weight at a temperature of 7.5°C. These were obtained as part of a larger, in progress, study of growth, feeding and metabolism of j.A.s. What is needed are measurements of standard, routine and active oxygen consumption from near 0°C to the upper thermal limit. This information can then be used to construct balanced energy budgets, as outlined by Windell (1978), in which consumption can be estimated from the sum of energy accumulated in biomass, that proportion of food consumed which is not assimilated, that excreted and that used in respiration. The book edited by Tytler and Calow (1985) on fish energetics contains many suggestions applicable to study of j.A.s. The chapter by Priede (1985) is particularly instructive. He presents a formula to normalize metabolic data, $S = (R-R_S)/(R_{\max}-R_S)$, where S = power or metabolic rate normalized with respect to metabolic scope, R = routine metabolic rate, R_S = standard metabolic rate and $R_{\max}$ = active metabolic rate. S then ranges from 0 at R_S to 1 at $R_{\max}$. Fish, except for very short intervals, must operate between these limits, performance limits usually being set by the fishes ability to extract oxygen from water. Operating at the limits threatens survival. Routine metabolism can be partitioned into standard metabolism + metabolism due to activity + SDA (specific dynamic action) which is associated with digestion and biochemical processes involved in protein mobilization. Since, after feeding, SDA can account for a large component of the metabolic scope, there is a conflict in fish between activity and digestion. A 500 g brown trout at 15°C, operating at about 0.5 S, uses 340 mW, partitioned between 145 mW for standard metabolism, 177 mW for SDA and 18 mW for swimming. If it was swimming at maximum speed and digesting a full meal, it would consume 962 mW, but at $R_{\max}$ only 624 mW of power is available (Priede 1985). The implication is that, to feed and grow maximally, activity must be restricted. Atlantic salmon presumably act similarly. Their normal level of activity is low except for short excursions to capture prey. As densities increase, more energy is expended on interspecific interactions and SDA must be reduced by consuming less food and growth is retarded.

In larger species of fish, activity can be measured by radio telemetry (Priede and Young 1977). In small species other methods have to be used. Direct observation offers a way of collecting data on diet, feeding rate and activity. Stradmeyer and Thorpe (1987) used both shore and under water observation to examine feeding behaviour of j.A.s. in the River Tilt, Scotland. Prey were obtained from the surface, mid-water and the bottom; surface feeding was more prevalent in larger parr and decreased during rain. The way fish approached prey minimized energy expenditure except that fish often attacked prey too large to swallow. Prey ingested were swallowed with a quick snap and were hardly visible. Feeding frequency increased with temperature. Heggenes et al. (1991) compared river bank and underwater observations of microhabitat use by salmon and brown trout parr in a Norwegian stream. They found bias towards seeing more fish in shallow water from the bank and more fish in deeper, faster water by snorkeling. Rimmer et al. (1985) and Cunjak (1988) extended underwater observation through autumn and into winter in Canadian streams. In winter, j.A.s. occupy habitat in the middle of the channel in runs with unconsolidated substrate, which offers hiding places under stones and rubble. Cunjak (1988) observed feeding throughout winter and suggested j.A.s. are photonegative at low temperatures, foraging only at low light intensities.

There is no question about the value of seeing what j.A.s. do directly, and it would clearly be useful to extend the range of underwater observation. I have found no references to use of video technology for this purpose. Cameras installed adjacent to "home stations" could be programmed to take pictures at intervals during 24 h. With playback, stop frame and zoom capabilities, it might be possible to identify and count prey and record diel patterns of consumption. Energy expended in activity including interception of prey could be estimated from tail beat frequencies, or swimming speeds and distances, once these had been correlated with oxygen consumption rates in a tunnel respirometer. Tapes providing a record of observation can be subject to more critical analysis than direct observations which are limited by the stamina and patience of the diver and depend on visual acuity and memory. Such an approach should enhance our knowledge of the trophic relations of j.A.s. and meet with general approval since no valuable wild fish need to be sacrificed to obtain data.

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High Winter Discharge after Regulation Increases Production of Atlantic Salmon (*Salmo salar*) Smolts in the River Orkla, Norway

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HVIDSTEN, N. A. 1993. High winter discharge after regulation increases production of Atlantic salmon (*Salmo salar*) smolts in the River Orkla, Norway, p. 175–177. *In* R. J. Gibson and R. E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

Estimated smolt production has increased considerably in the period after hydro-power development in the River Orkla. The low winter discharges increased about five-fold after storage regulation. Smolt production during and after regulation is positively influenced by high winter disharges. The smolt production has probably increased due to reduced mortality during the ice-covered period, and as a result of increased food items at elevated minimum water levels.

La production estimée de smolts a augmenté considérablement dans la période qui a suivi le développement hydroélectrique dans la rivière Orkla. Les débits d'hiver, qui étaient faibles, ont été multiplés par cinq après la régularisation de la retenue des eaux. La production de smolts pendant et après la régularisation est positivement affectée par les forts débits d'hiver. La production de smolts a probablement augmenté à cause de la baisse de la mortalité pendant la période où l'eau est couverte de glace, et à cause de la hausse de la quantité de nourriture du fait que les basses eaux étaient plus hautes.

Introduction

The River Orkla was developed for hydro-power production in 1983. Winter discharges were increased compared to unregulated conditions. Annual smolt productions were estimated in the period from 1983 to 1991 (Hvidsten and Ugedal 1991). Estimated smolt production has increased in the period following regulation. We discussed the possibility that increased winter discharges might be the main limiting factor for smolt production in the river Orkla (Hvidsten and Ugedal 1991).

Production of salmonids in running water is dependent on a number of factors. Gibson and Myers (1988) found that survival of salmonids and winter discharges were related in six rivers in Newfoundland and New Brunswick. Precipitation in the form of snow provides low winter discharges in the River Orkla. In the present paper, we tested the hypothesis that smolt production should increase as the winter discharge increased following regulation.

Methods

Smolt production was estimated in the period from 1983 through 1991, with the exception of 1989. Estimates of smolt production were performed according to Ricker (1975) , and the methods are described by Garnås and Hvidsten (1985) and Hvidsten and Ugedal (1991). Water discharges, recorded by The Norwegian Water Resources and Electricity Board, discharges are described as mean water discharge per day. An index of the lowest recorded discharges through the winter (January through March), usually occurring in late winter (March), were related with eight years of smolt production. The influence of the last and the two and the three winter discharges prior to the smolt run were analysed separatly. Indicies of water discharges representing the lowest winter discharges during the life of the smolts were correlated to the smolt production. The salmon smolts are three and four years old when leaving the River Orkla (Hvidsten 1990). The index representing each year was the quotient between the low water discharge of the year and the mean of the low water values of these years (1981–91). Linear and other curve correlation analyses were performed.

Average discharge throughout the year is 41 m^3s^{-1}. The lowest natural discharges varied down to 1–2 m^3s^{-1} in the winter, and upward to about 1000 m^3s^{-1} during the spring floods. After regulation, water discharge is never below 10 m^3s^{-1} and the spring flood has not exceeded 300 m^3s^{-1}.

The Atlantic salmon is the predominant species in the River Orkla. Migrating brown trout averaged 10 % (in numbers) in the period between 1980 and 1988 (Hvidsten 1990).

Results

Smolt production was related to the lowest discharges for the two and three winters prior to the smolt run ($r=0.81$, $p<0.025$ and $r=0.75$, $p<0.05$ respectively). The correlation was best when using the two last winter discharges before the smolt descent (Table 1, Fig. 1). When correlating the final winter's discharge separately with smolt production, the influence was insignificant ($p>0.05$).

TABLE 1. Smolt production per 100 m^2 and lowest daily water discharges 1–3 winters before smolt migration in the River Orkla in m^3s^{-1}, and index and multiplied index for the water discharges two and three years before the smolt run. n = discharge the last winter before descent, $n - 1$ = discharge two winters before descent, $n - 2$ = discharge three winters before descent.

Year	Lowest mean water discharges								
	smolt prod (c.i.=.95)	n m^3s^{-1}	n/Σn index A	n-1 m^3s^{-s}	n/Σn index B	n-2 m^3s^{-1}	n/Σn index C	A×B	A×B×C
83	4.0 (2.7–6.1)	11.1	0.76	2.2	0.15	1.7	0.12	0.12	0.01
84	6.1 (4.4–8.8)	20.1	1.38	11.1	0.76	2.2	0.15	1.05	0.16
85	5.8 (3.6–8.8)	15.5	1.07	20.1	1.38	11.1	0.76	1.48	1.12
86	7.6 (4.9–12.1)	11.6	0.80	15.5	1.07	20.1	1.38	0.86	1.18
87	7.9 (6.2–10.1)	12.1	0.83	11.6	0.80	15.5	1.07	0.66	0.71
88	5.1 (3.9–6.5)	14.3	0.98	12.6	0.87	11.6	0.80	0.85	0.68
90	10.8 (7.8–15.3)	20.1	1.38	34.2	2.35	14.3	0.98	3.24	3.18
91	8.1 (6.8–9.6)	17.1	1.18	20.1	1.38	34.2	2.35	1.63	3.83
			r=0.47					r=0.81	r=0.75

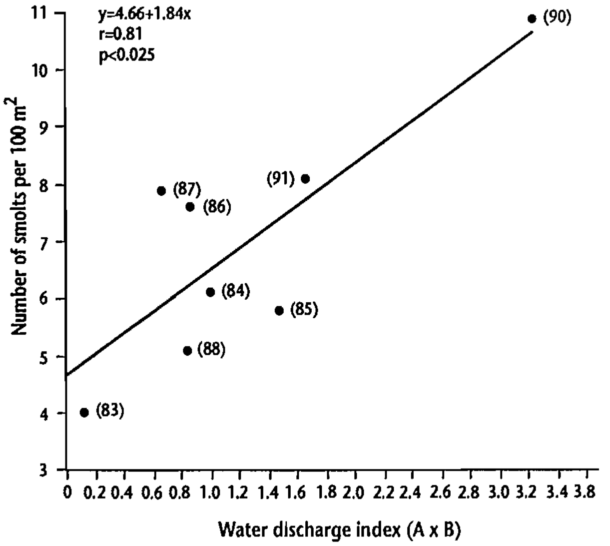

FIG. 1. Salmon smolt production and low winter discharge index in the River Orkla.

Discussion

Smolt production estimates were performed for 8 years, prior to and within the period of regulation for hydropower production. Winter discharges under regulation are higher than natural winter discharges. Smolt productions were on average, estimated to be 1.8 times higher as the winter discharges increased five-fold after regulation (1983–91). The increase in the smolt production is probably even higher because the smolts experienced elevated water discharge in the winter of 1983.

In two to three of the latest winters, lowest discharges prior to the smolt run influenced the number of smolts produced. These results accord with a smolt age of 3 and 4 years, and the final smolt production depends on high winter survival during years prior to descent.

In a review of other authors, Hearn (1987) suggests that stream-dwelling salmonid populations may be limited at different times by competition, predation, or climatic events, such as droughts or floods. Following regulation of the River Orkla, the water discharge is elevated in the winter from 1–2 m^3s^{-1} to minimum discharges of 10 m^3s^{-1}. Allen (1941) and more recent authors have reported that juvenile salmonids seek cover in the bottom substrate when water temperatures drop below 7-10°C in the autumn. Mortality of salmon parr is caused by inter- and intraspecific competition limited by river bed habitats (Kalleberg 1958; Rimmer et al. 1983; and Heggenes and Saltveit 1990). Each parr inhibits a substrate chamber (Rimmer et al. 1983). As water discharges increase, more substrate chambers are available through the winter. Natural mortality and migration in migratory brown trout 0+ population are extremely high as survival averaged

41% the first winter (Elliott 1985). We hypothesize that when the unregulated rivers are covered with ice at relatively high water discharges early in the winter, parr can be trapped in their substrate chambers by ice as the water level decreases during the coldest period in the winter. Presmolts may be stranded in shallow parts of the river where ice cover prevents escape when water level drops below their hiding sites. Presmolts may then freeze to death or die from oxygen deficiency. High mortality probably occurs in natural river systems in years when the water discharge drops during periods with freezing temperatures. This finding may accord with Gibson and Myers (1988) who reported positive relationships between survival of underyearlings and winter discharge in six rivers in Newfoundland and New Burnswick. Winter discharges are low in boreal areas compared to more southern parts of the salmonid distribution area. In the neighbouring River Nidelva, which has regulated water discharges, salmonids of the year were stranded even before they sought cover in the substratum during periods of sudden and high reduction in water discharge (Hvidsten 1985).

The findings in River Orkla accord with the results reported by Saunders and Smith (1962) and Näslund (1987) who reported that elevated water levels after building wiers increased salmonid survival through the winter. Elevated regulated discharges in the River Nidelva (min 30 m^3s^{-1}) probably give the highest catch of adult salmon in Norway. In certain years, one tonne of salmon are caught per kilometre of salmon-producing area.

The increase in permanently wetted areas after regulation in River Orkla has possibly contributed to higher carrying capacity of insects. Before regulation, large floods up to 1000 m^3s^{-1} could sweep many valuable insects into the sea. Catastrophic drift of insects associated with flood conditions is described by Brittain and Eikeland (1988), reviewing other authors. Following regulation, floods have never exceeded 300 m^3s^{-1}.

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Juvenile Atlantic Salmon (*Salmo salar*) — Production and Prediction

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The objective of this synthesis paper is to summarise recent research on salmon production models of whole river systems from both sides of the Atlantic. Three main topics are addressed. First, we collate evidence apposite to theoretical models of the freshwater stock-recruitment relationship of juvenile salmonids, including variation in reported survival rates and the influence of differing environmental parameters, both between and within catchments. Secondly, we review the work in progress on various index rivers, with an evaluation of how the results to date relate to existing stock-recruitment models. Finally, we assess the value and limitations of the information now available on juvenile salmon population dynamics for the prediction of smolt yields, along with a discussion of future research requirements. Data from the R. Bush are presented to illustrate the relevant salmonid research presently being carried out in Northern Ireland.

L'objectif de notre travail de synthèse est de résumer les recherches récentes sur les modèles de production du saumon dans un système lotique complet, des deux côtés de l'Atlantique. Trois grands sujets sont traités. Premièrement, nous colligeons des preuves étayant des modèles théoriques sur la relation stock-recrutement en eau douce chez les salmonidés juvéniles, notamment la variation dans les taux de survie signalés et l'influence de paramètres environnementaux différents, tant à l'intérieur des bassins hydrographiques qu'entre eux. Deuxièmement, nous examinons les travaux en cours sur divers cours d'eau indicateurs, en évaluant la façon dont les résultats recueillis jusqu'à maintenant concordent avec les modèles actuels stock-recrutement. Enfin, nous évaluons l'intérêt et les limitations de l'information qui existe sur la dynamique des populations de saumons juvéniles pour la prévision de la production de smolts, tout en analysant les besoins futurs de la recherche. Les données recueillies sur la rivière Bush servent à illustrer la recherche actuellement menée dans ce domaine en Irlande du Nord.

Introduction

It is now clear that juvenile salmonid dynamics is a function of temperature, rainfall patterns, underlying geology and substrate types, water quality, catchment land use, predation and competition from sympatric species at least as much as intra-specific control mechanisms (see Gibson 1988 for review). Much of the detail on the nature of regulating mechanisms and how they function in different parts of the world is the subject of other areas of this symposium. In this paper we intend to give an overview of the state of the art of salmon production modelling at the river system level, rather than at micro-habitat level. We will draw on the results we have obtained in the R. Bush in Northern Ireland (see Fig. 1), where research into the ecology and population dynamics of salmon has now been in progress for 18 years. The trends emerging in this catchment will be compared to other rivers on both sides of the Atlantic. How close are we to a full understanding of all the factors controlling production and to the provision of meaningful models on which stock management can be based? How comparable are the models from different rivers? What is the applicability of models derived from so-called 'index rivers'(Anon. 1985)? Is the policy of focussing attention on such catchments the most appropriate way forward for the estimation of national smolt yields and the assessment of overall production?

Shape of the Freshwater Stock-Recruitment Relationship

The debate as to the precise shape of the ova to smolt stock-recruitment relationship for salmon is still ongoing. A good review of the historical evidence available for both the dome shaped and flat topped curves was given by Solomon (1985), who concluded that the flat topped version was the most appropriate for juvenile salmon. However, Solomon's conclusion was not unequivocal, and he postulated that at the existing levels of monitored stocks the data are mostly from the lower end of the range of the stock-recruitment model — well away from any possible right hand descending limb.

More recently, data have become available from several monitored rivers for smolt production at a higher range of ova depositions. In Western Arm Brook in Newfoundland, Chadwick (1991) reports that the numbers of smolts per spawner are in the range 28–53 at low spawning densities, and much lower at 8-14 smolts per spawner at high spawning densities. A similar reduction in smolts per spawner

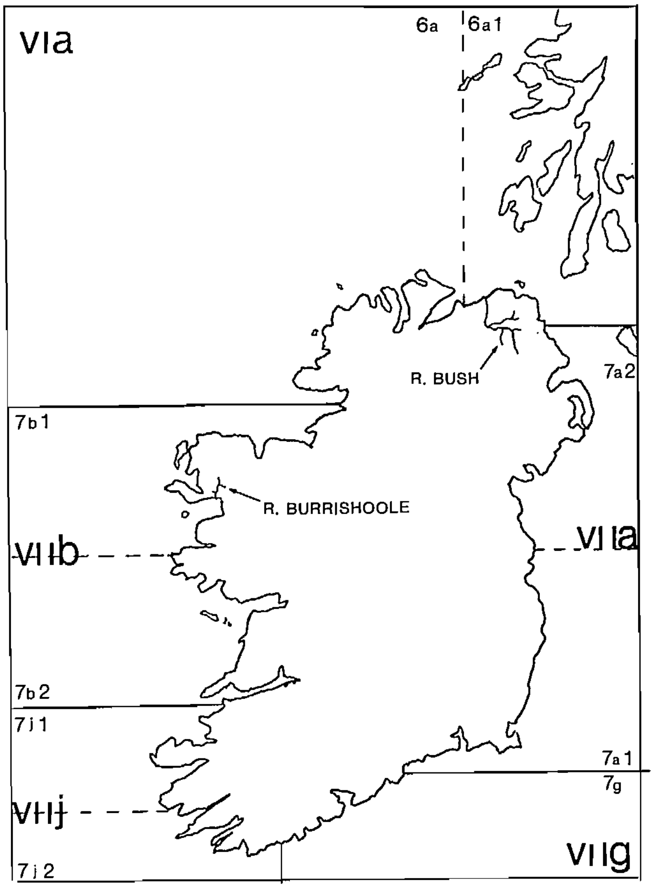

FIG. 1. Ireland showing position of the Rivers Bush and Burrishoole.

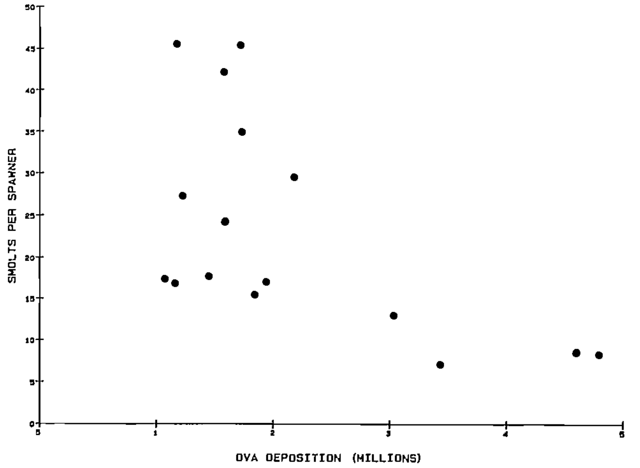

FIG. 2. Number of smolts per spawner plotted against varying ova depositions on the R. Bush, 1973–87.

at high ova depositions has been found on the R. Bush (Fig. 2). However, this in itself does not clarify the shape of the stock-recruitment relationship.

In a 6-yr study on the Shelligan Burn in Scotland Gardiner and Shackley (1991) report that densities of emergent salmon fry > 20 m^{-2} depressed subsequent recruitment, and that the survival of fry to the first and second autumns was consistent with a dome shaped Ricker curve. However, Hay (1991) outlines the dangers of interpreting short term data sets, and presents a rather different interpretive approach to a data

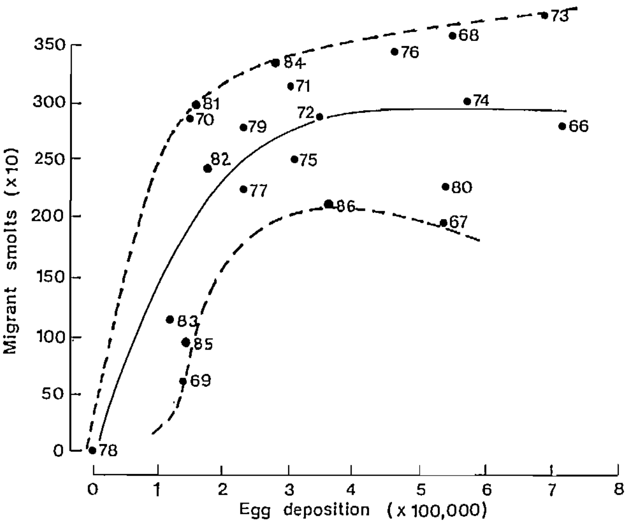

FIG. 3. Total smolt counts on the Girnock Burn from varying ova depositions, 1966–86. The dotted lines define the envelope of production proposed by Hay (1991). (Redrawn with the kind permission of D. Hay, Scottish Office, Agriculture and Fisheries Department).

series running since 1966 on the Girnock Burn in Scotland. He reports that at high ova depositions an 'envelope' bounded by diverging upper and lower lines defining the limits of smolt production best represents the stock-recruitment relationship (Fig. 3). Hay considers that in years when adult salmon penetration of spawning streams is good, their eggs are spread uniformly over a wide area, and smolt production tends towards the upper edge of the envelope. Conversely, in years when spawning is restricted to smaller areas and initial juvenile densities are localised, smolt production is reduced. Ongoing research into the environmental variables involved suggests that this effect is regulated by rainfall and river flows, with 'windows of opportunity' for spawning in different stream areas being related to certain optimum water levels at critical periods (Hay 1989).

Comparisons Between Rivers

(i) Smolt Count Data

Smolt counts are available for a large number of rivers on both sides of the Atlantic, both from trap counts and mark-recapture estimates, e.g., Ireland: R. Bush (Crozier and Kennedy 1991a), R. Corrib (Browne 1990), R. Burrishoole (Anon. 1990); Scotland: N. Esk (Shearer 1986), Girnock Burn (Buck and Hay 1984); Atlantic Canada: Western Arm Brook, Little Codroy R., Sandhill R., Big Salmon R., Black R. (Chadwick 1985a, 1988, 1991). The numbers vary widely, both between systems and within rivers in different years. The former is hardly surprising, given the great variation in sizes, productivity and smolt age structure of the various rivers. The annual fluctuations represent both density dependent and density independent variables, and these can result in within river variation in absolute smolt numbers of up to about six fold.

No correlations in absolute smolt numbers have been detected between river systems in the British Isles in equivalent years. However, Chadwick (1988) reports that in Newfoundland, returns of adults to neighbouring Grand Codroy and Little Robinson rivers can be predicted from Little Codroy smolts, and that Western Arm Brook smolts can be used to predict total returns to local home waters — where they represent 10% of the stock. Chadwick (1985b) also reports that counts of grilse in the Torrent River are correlated with counts of smolts in Western Arm Brook the previous year. These findings imply correlations in absolute smolt numbers in neighbouring rivers. Examination of such data series is fundamental to the concept of utilising smolt counts on certain rivers as an index of the dynamics of other local stocks. There is a paucity of published information on such data series, and no information at all on the geographical extent of such parallel stock fluctuations.

(ii) Ova to Smolt Survival Data

Another way of looking at the production data from salmon rivers is in terms of the ova to smolt survival from each cohort. This is only available for index rivers where accurate information on adult numbers, age structure, sex ratio and fecundity is available in addition to smolt counts. On the River Bush ova depositions and smolt counts have been monitored since 1973, and the temporal trend for ova to smolt survival is shown in Fig. 4. Survival has varied from 0.40 to 2.13%, with the lowest values resulting from the 1986 and 1987 ova depositions. These data can be compared to the ova – smolt survival values recorded over the same time period in the other Irish index river, the Burrishoole (Fig. 4). Three main conclusions can be drawn:

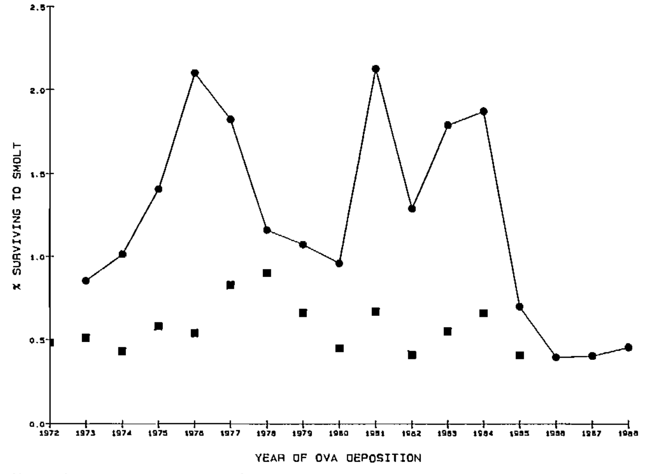

FIG. 4. Percentage survival from ova to smolt for each ova deposition on the R. Bush, 1973–88 (circles and solid line) and on the R. Burrishoole, 1970–85 (squares and dotted line). (The R. Burrishoole data are taken from the means of the published ranges of ova to smolt survival for this river (see Anon. 1990)).

(a) There is no overall significant correlation in the annual ova to smolt survival data between the two rivers over the period 1973–1985 ($r = 0.39$). However, the most obvious divergence in survival between the two systems occurred in 1978, when Burrishoole survival rose to its highest recorded value, whereas Bush survival dropped sharply. If this outlier is excluded, all the others years do show a significant correlation in their ova to smolt survival ($r = 0.61$; $p < 0.05$).

(b) The maximum and average survival from ova to smolt on the R. Burrishoole is less than half that on the R. Bush.

(c) The level of annual variation in the R. Burrishoole ova to smolt survival (from 0.39% to 0.95%) is only about half that recorded in the R. Bush.

The lack of correlation in freshwater survival rates between the two rivers in all years suggests that the factors influencing annual production can be very local in their effects. However, the data imply that there is also an overlying regulating mechanism influencing ova to smolt survival similarly in both rivers over a long time series. Presumably the mechanism is environmental, possibly related to rainfall and the effects of river flow on the distribution of spawners, as appears to be the case in the Girnock Burn (Hay 1989, 1991). High flows can also cause washout and siltation of redds, and low flows result in the stranding of redds (Harris 1978) or the limited dispersal of emerging fry (Kennedy 1988). However, temperature may also play a part, and in the less temperate climate of Newfoundland, Chadwick (1982) reported significant inverse correlations of egg to fry survival with both river discharge and winter temperature. Apparently extreme winter temperatures caused freezing of redds at low river levels causing high egg mortalities. Chadwick attributed the very low smolt production from the 1972 year-class on Western Arm Brook to these extreme weather conditions.

Comparison of the R. Bush and R. Burrishoole data further indicates that two rivers within the same geographical region (catchments separated by about 250 km) can also show great differences in their productivity — as measured by ova to smolt survival. The productivity of streams for salmonids is related to the level of enrichment and the resultant standing crop of invertebrate food organisms available (Mills 1989; Symons 1979). The R. Bush catchment land use is intensively agricultural, with associated enrichment by fertiliser and organic leachate, whereas the Burrishoole catchment is comprised of much poorer land, supporting only rough grazing, mainly for sheep. Land use patterns, the associated enrichment of streams and measures of primary productivity are seldom discussed in relation to salmon production in streams, but have important implications for estimating target ova depositions and the applicability of index river data to smolt production for neighbouring catchments.

A further difference between these two Irish index rivers is in the range of the variability in their ova to smolt survival from year to year. Freshwater survival rates have varied by a factor of 5.3 on the R. Bush to date, whereas the equivalent variation on the R. Burrishoole is by a factor of only 2.4. To determine whether this is due to density dependent or density independent mechanisms we must examine the stock-recruitment relationship for each catchment.

(iii) Smolt production from varying ova depositions.

On the R. Bush, ova depositions from 1973 to the present have varied from 1.07 million to 4.79 million. Of these, the bulk fell within the range 1.07 million to 2.18 million. Only in the four brood years 1985–1988 have ova depositions exceeding 3 million been achieved — as a consequence of enhancement efforts on the river (Kennedy and Crozier 1989). Total smolt counts of 1+, 2+ and 3+ smolts from each ova deposition are therefore only available up to the brood year 1987 (Fig. 5a). (Since 3+ smolts comprise <1% of the total to date, the count of 1+ and 2+ smolts from the 1988 ova deposition have also been included.) A Ricker curve has been fitted to the data. There are two main points to be made:

(a) There has been a wide range of smolt production from the lower end of the range of ova depositions (up to 2.18 million).

(b) The smolt production to date from the years where ova depositions exceeded 3 million has been at the lower end of the range.

At this point in the time series the results therefore suggest a dome shaped density dependent stock-recruitment relationship, with density independent variation producing a wide scatter of points, particularly on the ascending limb of the curve. However, Hay's (1989, 1991) findings on the Girnock Burn, indicate that density independent variability at high ova depositions can also cause large annual variation in smolt production. Chadwick (1991) came to a similar conclusion for the Western Arm Brook and Black River, where he noted that at high stock densities the production of smolts became 'unpredictable'. Chadwick also noted that the smolt size at age declined with increasing ova deposition in Western Arm Brook, but that mean smolt age did not change. The converse appears to be the case on the R. Bush, where no trend has so far been detected in mean smolt size at age with increasing ova deposition, but the age structure of the smolt run has altered significantly. At the four ova depositions > 3 million to date 1+ smolt output has been very low on the R. Bush, compared to an apparent steeply sloped ascending limb of 1+ production rising to a peak of potential 1+ production at ova depositions in the approximate range of 1.6 million to 2.2 million (Fig. 5b). This, in itself, has reduced overall smolt production and resulted in the apparent dome shaped stock-recruitment curve for the R. Bush (Fig. 5a), since 2+ smolt production has been maintained within the 'normal' range at ova depositions >3 million (Fig. 5c). No detectable trend in 3+ smolt numbers has been evident throughout the various ranges of ova deposition on the R. Bush, and these have formed <1% of the run overall. The results therefore indicate an absolute reduction in the 1+ age class at higher ova depositions, and not a shift in age structure from 1+ to 2+ or 3+.

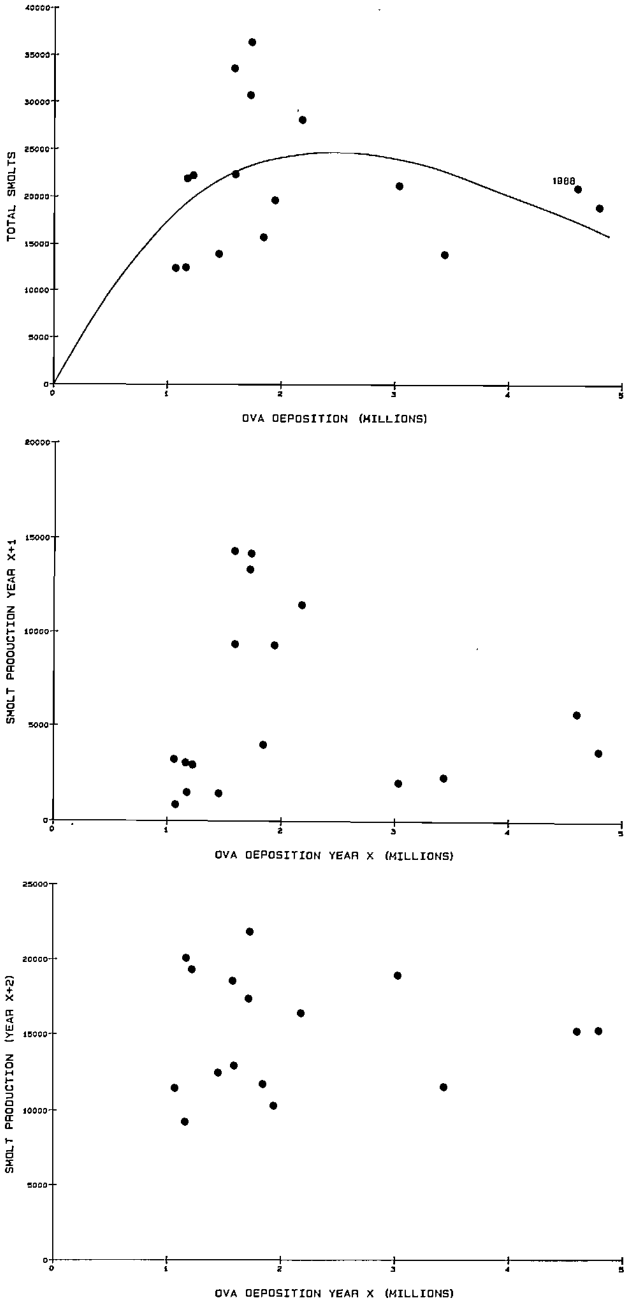

FIG. 5. (a) Total smolt counts on the R. Bush from varying ova depositions, 1973–88. (The 1988 data point excludes 3+ smolts, for which counts are not yet available, but which comprise <1% of the total annual run). A Ricker curve has been fitted to the data ($r^2 = 0.915$; $p < 0.001$). (b) Counts of 1+ smolts on the R. Bush from varying ova depositions, 1973–89. (c) Counts of 2+ smolts on the R. Bush from varying ova depositions, 1973–88.

It is therefore possible that the few data points obtained to date at high ova depositions on the R. Bush represent only the lower range of the smolt production values possible from these ova depositions — due to unfavourable density independent factors in recent years. Time will tell, but the point to be learned here is that there is a continuing need for a long time series of data in this type of work, and, as emphasised recently by Hay (1991), considerable dangers for salmon biologists in being tempted to interpret too much from short term data sets.

On the R. Burrishoole the smolt production over a range of ova depositions from about 0.5 million to > 3 million are shown in Fig. 6. It appears from this data set that the asymptote of the stock recruitment relationship has not yet been reached on the Burrishoole — a conclusion which largely explains the apparent difference in the magnitude of the variation in freshwater survival rates between the two systems. On the analogous ascending limb of the stock-recruitment relationship for the R. Bush (up to an ova deposition of 2.18 m), ova to smolt survival ranged from 0.85 to 2.12%, ie variation by a factor of 2.5 (cf variation by a factor of 2.4 in ova to smolt survival in the R. Burrishoole).

On Western Arm Brook Chadwick (1991) reported that at low spawning escapements 28 to 53 smolts were produced per spawner ie a 1.9 fold variation. This led Chadwick (1988) to conclude that at low and medium stock densities most variation in the production of smolts can be explained by egg deposition. He notes that, in Newfoundland, variation in sea survival is much greater than variation in freshwater survival and suggests that 'further research on factors other than egg deposition which control smolt production will not necessarily improve our ability to predict returns of adults'. While this may be generally true in Newfoundland, nevertheless extremes of freshwater density independent variation, such as appeared in the 1972 year-class in Western Arm Brook, can occur. Furthermore, a variation of 2.5 fold in freshwater production on the R. Bush, attributable largely to density independent factors, equates to a variation in smolt production from about 14,000 to 35,000 smolts from a low ova deposition (see Fig. 5a). We would suggest that this is not an acceptable level of unpredictable variability, and recommend that further research on the causes of density independent mortality in freshwater should not be neglected.

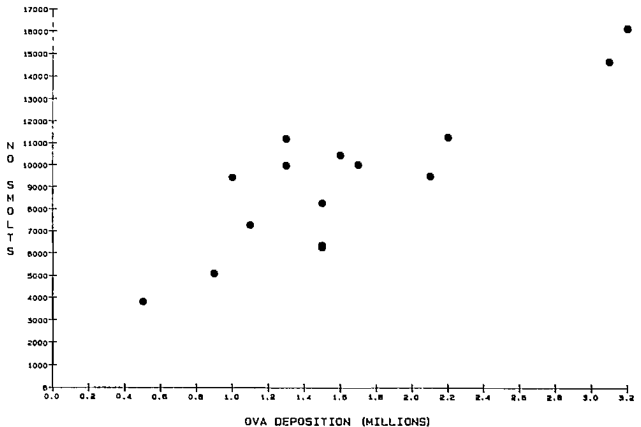

FIG. 6. Total smolt counts on the Burrishoole from varying ova depositions, 1970–85. (The ova depositions are taken from the mean of the published ranges for the R. Burrishoole (see Anon. 1990)).

This conclusion is given further emphasis by the fact the marine survival rates of R. Bush smolts are much less variable than the figure of twenty fold reported for Western Arm Brook (Chadwick 1991). Total adult return to the R. Bush has varied from 3.9 to 12.0% from 1974–1989 (ie a 3.1 fold variation), and return to the coast prior to exploitation has been assessed at 25.0 to 36.2% (i.e. < 1.5 fold variation) for grilse stocks from 1987 to 1989 (Crozier and Kennedy, in prep).

Also, from the evidence available to date (Hay 1991), high density independent fluctuations in ova to smolt survival are also found above the asymptote of the stock-recruitment curve. More information is therefore required from monitored rivers at high ova depositions, and identification of the position of the asymptote is a basic requirement for each system if target ova depositions are to be set.

The next question is therefore how comparable are various monitored rivers in terms of their smolt production, and what are the target ova depositions necessary to achieve these production potentials?

(iv) Target Ova Depositions

Whether the salmon freshwater stock-recruitment curve is flat topped or domed, the smolt production capacity of a river system only becomes apparent at the asymptote of the curve. This area of inflexion indicates the minimum number of eggs which have the potential to produce the maximum number of smolts from a river system, given optimum density independent survival conditions. This is known as the target ova deposition, and is not synonymous with the potential egg deposition of the adult freshwater escapement. The freshwater exploitation rates from sport fisheries vary greatly between systems (Mills 1991) and the extent and variation of non-catch fishing mortality and natural mortality in freshwater is unknown. Elson (1975) suggested that a figure of 25% freshwater mortality should be applied to cover these losses, and this appears to have become a standard in the absence of hard data.

This freshwater mortality correction factor has been incorporated into the recommended egg deposition rate of 2.4 ova m^{-2} now used as a basis for calculating target spawning requirements in Atlantic Canada. Chadwick (1985b) questioned the applicability of this rate to all rivers, without taking account of unique local factors. Certainly, Elson's (1975) warnings of the dangers of exceeding the recommended density of 2.4 m^{-2} have now been largely discounted due to a general lack of acceptance of his proposed steeply domed stock-recruitment curve (Chadwick 1982, 1985b; Solomon 1985). From the evidence now available it seems certain that, due to limited data at high ova depositions, Elson misinterpreted density independent variability in R. Foyle stocks for a downward trend in numbers beyond the asymptote of the curve.

On the R. Bush the evidence to date suggests that the asymptote of the stock-recruitment curve occurs at an ova deposition < 3 million. The highest values of ova to smolt survival recorded indicate that the asymptote may well lie in the region 1.6 to 2.2 million. The fitted Ricker curve suggests that the asymptote may occur at a slightly higher ova deposition (about 2.4 million (Fig. 5a)). However, more data points are required at medium to high ova depositions as the range of density independent variation is sufficiently large to mask more precise assessment.

Given the imprecision in assessing the position of the asymptote of the salmon stock-recruitment curve due to density independent variability, it is inappropriate to express target ova deposition as a single recommended figure for any system. There are also a variety of ways in which target ova deposition may be expressed in relation to particular catchment and habitat definitions. For example, the whole catchment range of 1.6 million to 2.4 million target ova deposition for the R. Bush can also be expressed as illustrated in Table 1. These may be more appropriate for comparision with other rivers where the proportions of different habitat types may vary greatly. For example, the Girnock Burn is an upland tributary with a catchment of 2800 ha, and 5.8 ha of useable salmonid habitat (D. Hay, pers. comm). The asymptote of the stock-recruitment curve on this system lies within a range of about 200,000 to 300,000 ova (see Fig. 3), and this is equivalent to an ova deposition of 71.4 to 107.1 ha^{-1} of catchment or 3.5 to 5.2 m^{-2} of usable salmonid habitat.

The capacity of different habitat types in streams of differing productivity to accommodate different ova depositions was emphasised by Symons (1979), who related this to a range of smolt production levels. From a literature survey he suggested that smolt production varied from about 0.01 to 0.1 m^{-2} annually for whole streams, and his recommended overall target ova depositions varied from 0.8 to 2.2 m^{-2}. However, he recognised that smolt production and target ova depositions could be higher for restricted areas of productive nursery habitat. Mills (1989) recorded higher smolt production figures of up to 0.116 m^{-2} in the R. Tweed and 0.22 m^{-2} in the Shelligan Burn, and Kennedy (1985 and in prep.) considered that annual smolt outputs of >0.3 m^{-2} were possible from stocking densities of 6.2 m^{-2} in the highly productive nursery habitat found in the Altnahinch tributary of the R. Bush. Smolt production from the R. Bush as a whole has varied considerably, and as for ova deposition data, can be expressed in a variety of different ways depending on the habitat types targeted (see Table 1).

It is evident therefore that one recommended egg density is also inappropriate for all habitat types within any one system, and that any recommended target ova deposition is highly dependent on the proportion of different types of habitat in different river systems. This was recognised by Chadwick (1985b), who emphasised the need for more intensive surveying of habitat types in river systems prior to recommending target ova depositions. He was particularly critical of surveys which excluded lacustrine habitat, which he reported could account for up to 70% of smolt production in some systems. Einarsson, Mills and Johannson (1990) similarly found that juvenile salmon were recruited to Lake Medalfellsvatn in Iceland, apparently mainly by upstream migration from spawning sites in the outlet stream. These authors noted the paucity of data on this aspect in Icelandic rivers, but considered that since lakes were abundant, lacustrine smolt production could be 'significant' there.

Evidence for the importance of lakes for smolt rearing is also available in Ireland. Although the Burrishoole has a lower ova to smolt survival than the R. Bush, the maximum annual smolt output recorded to date on the Burrishoole (apparently below the asymptote of the stock-recruitment relationship here — see Fig. 6) is 1.75 ha^{-1}, which is higher than that for the R. Bush (1.08 ha^{-1} (Table 1)). The difference appears to be the result of production arising from parr residing in Lough Feeagh (410 ha) in the Burrishoole catchment — the R. Bush having no comparable standing water in its catchment. It is therefore clear that while rearing habitat may be an adequate measure of stock productivity, it is not necessarily comparable between catchments, and detailed field surveys are required on all systems before target egg depositions are calculated.

TABLE 1. Options for expressing (a) target ova depositions in the range 1.6–2.4 million for the R. Bush and (b) ranges of annual smolt production observed on the R. Bush.

Habitat type	Area in R Bush catchment	Target ova deposition	Range of smolt production
Total river catchment	33,700 ha	47.5–71.2 ha^{-1}	0.37–1.08 ha^{-1}
Total wetted surface of river	84.55 ha	1.9–2.8 m^{-2}	0.015–0.043 m^{-2}
Total usable salmonid nursery habitat	41.06 ha	3.9–5.8 m^{-2}	0.030–0.089 m^{-2}
Total usable grade A salmonid nursery habitat	23.38 ha	6.6–9.8 m^{-2}	0.051–0.149 m^{-2}
Total area of grade A salmonid nursery habitat normally used	16.91	9.5–14.2 m^{-2}	0.073–0.215 m^{-2}

More fundamental research is required to define habitat types more closely and to determine the egg depositions which are appropriate for these in both running and standing waters. In a previous paper Kennedy (1988) reviewed the egg and fry densities employed during various enhancement stocking schemes, and noted the lack of a systematic approach. The most comprehensive recommendations made for artificial stocking densities in relation to habitat type and productivity have been produced for Scottish streams by Egglishaw et al. (1984). These range from 2 to 10 ova or unfed fry m^{-2} depending on the productivity, altitude and size of the streams. However, there is evidence that natural ova depositions should not be equated to those calculated from artificial stocking (Kennedy 1988). Apparently the careful dispersal of eggs and fry during stocking operations can improve survival by over three fold compared to the natural mortality rates induced by clumping of adult spawners, and the subsequent limited dispersal of fry from spawning sites (Kennedy 1988; O'Connell et al. 1983). However, the parameters involved in regulating survival from stocking operations have never been satisfactorily quantified, and recommended artifical stocking densities and natural ova deposition rates are frequently cited in the literature as if they were synonymous.

Modelling and Prediction

On the R. Bush the availability of total trapping facilities has enabled us to assess the effectiveness of electrofishing as a measure of juvenile recruitment and smolt production. Early work using fully quantitative electrofishing in small numbers of stop-netted sites highlighted the limitations of this technique (Kennedy 1981). It was found that while the population estimate within the stop nets may be obtained very accurately, the methodology was very labour intensive, and the results may bear very little relation to the densities throughout the rest of the stream being sampled. A semi-quantitative single anode electrofishing technique using two man teams to sample O+ fry only over a large number of sites was therefore developed (Kennedy and Crozier 1991a). The fry indices obtained from this to date mirror the tendency for reduced survival at higher stock densities noted from the smolt counts (Fig. 7a). This suggests that the major factors influencing survival and stock-recruitment act prior to the summer O+ stage. This is further corroborated by the good correlation of summer O+ abundance indices to the following years' 1+ smolt production (Fig. 7b). This correlation is good evidence that at low manpower cost, this semi-quantitative technique does indeed provide an accurate reflection of recruitment to the river. The technique also enables comprehensive recruitment mapping of the entire catchment. However, although the technique has proved to be a useful predictor of 1+ smolt production, the results have as yet provided no indication of the causes of the high variability in the production of this age class over varying ova depositions.

Correlations of fry indices to 2+ and overall smolt production are not significant on the Bush, possibly indicating that further density independent factors can influence survival after 1+. On the R. Bush significant predation by cormorants, *Phalacrocorax carbo* L., occurs on the older parr and smolt stages (Kennedy and Greer 1988), and this may be influential here. The importance of local factors influencing density independent mortality have already been highlighted in relation to variability in ova to smolt survival between the rivers Bush and Burrishoole. The conclusion must therefore be that juvenile salmon estimates can be useful as predictors of smolt production within catchments. However, further research is required to assess the value of juvenile population estimates from monitored catchments as indices of smolt production in a wider geographical area.

In an earlier paper (Kennedy and Crozier 1988) we evaluated the concept of scaling up data on smolt

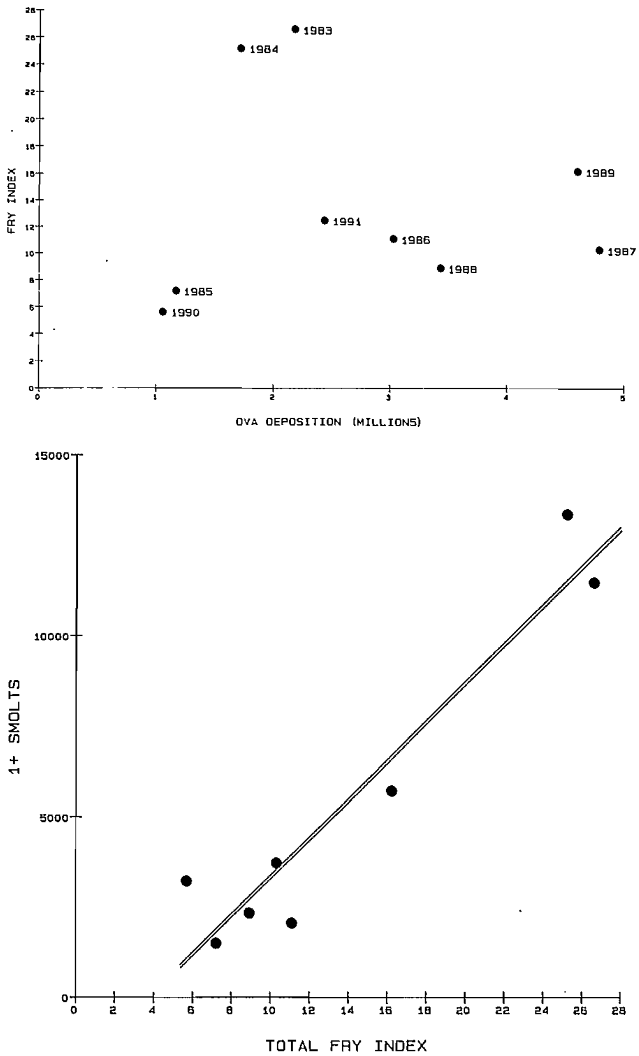

FIG. 7. (a) Abundance indices for 0+ salmon in the R. Bush at varying ova depositions from 1983–90, acquired by semi-quantitative electrofishing surveys. (b) Counts of 1+ smolts on the R. Bush from 1984–90 correlated with the previous year's index of fry abundance ($r^2 = 0.904$; $p < 0.001$).

production and marine mortality from the R. Bush to a model covering Northern Ireland's salmon production as a whole. The available salmon producing areas of river catchments presently used within N. Ireland were calculated on the basis of a desk study. Estimates of total smolt numbers were produced by applying the range of smolt production per hectare of catchment found on the R. Bush. Adult returns to homewaters and commercial exploitation rates in N. Ireland's waters were taken from microtagging data from the R. Bush and the likely range of annual commercial catches calculated. Using the most recent data available (Crozier and Kennedy 1991b), the predicted range of commercial landings from the model is approximately 35,000 – 232,000 grilse and multi-sea winter salmon. The actual landings to N. Ireland's commercial netsmen have ranged from 35,000 – 199,000 fish over the last 25 years (including non-catch fishing mortality estimates). The results therefore indicate that projections from the R. Bush as an index river for N. Ireland are on the high side, but in the correct order of magnitude. However, what is also clear is that there is potentially almost an order of magnitude difference between the extremes of the range for potential annual production.

A model has also been produced which includes the range of ova to smolt survival on the R. Bush to date (Kennedy and Crozier 1991a), and here the potential grilse production from 1 million ova varies by over an order of magnitude (from 131 to 2786). Subsequently we used this approach to indicate the ranges of marine exploitation which would permit annual ova depositions to fall within a suggested target range on the R. Bush (Kennedy and Crozier 1991b). R. Bush data was also used as input to a spreadsheet run reconstruction model proposed by Potter (1989) for assessing extant stock at various stages of the marine phase (Anon. 1989).

The common feature of these models is that they are all based on estimates from retrospective range data, and they cannot be used for prediction without further inputs. In this paper we have tried to identify some of the gaps in our database, and to review the extent to which the information we now have may or may not be applied predictively — either within catchments or wider afield.

Conclusions for Indexing

(i) Target ova depositions: These have generally not been formulated on the basis of stock-recruitment models, even for index rivers. Further work is needed to identify the nature of the stock recruitment relationship in a wide range of rivers, and to quantify the appropriate ova depositions and distributions for differing habitat types and levels of river productivity. The importance of lacustrine habitat for salmon production is certainly now recognised, but detailed information on juvenile recruitment to lakes and comparative production models from these in different areas is not available. For optimum management, target spawning escapements cannot continue to be realistically set on the basis of one historical density applied across continents, in adjacent catchments or even in different portions of one catchment. Inappropriate target ova depositions may well be masked in the short term by the high annual variation in smolt output from rivers resulting from high levels of density independent mortality. There may also be changes in smolt size or age structure, but there is no concensus and the regulating mechanisms are not well studied or understood. The need for more and better understood models of stock-recruitment is self-evident.

(ii) Modelling survival: The high density independent variation in ova to smolt survival found both above and below the asymptote of the stock-recruitment curve for juvenile salmon is apparently greater in temperate than in boreal regions. However, the 1972 data from Western Arm Brook indicates that occasional large fluctuations can also occur in the latter. More information is required on the causes of density independent variation in ova to smolt survival. Work to date suggests that rainfall and temperature are the main regulating factors, but the data are patchy and do not yet form the basis for prediction in any system.

There is also evidence that climatic regulating mechanisms may have some common influence over salmon production in a number of catchments in one geographical region, but that this can be over-ridden by local catchment effects. No comparative studies have yet been undertaken to identify and calibrate the thresholds at which the various mechanisms operate, or to evaluate the extent to which index river data may or may not be applied to neighbouring catchments. Certainly no information is yet available to indicate the extent to which juvenile densities from index river surveys may be used as the basis for smolt prediction on a wider geographical basis. Smolt production data has been used for prediction of adult runs between catchments and in local geographical areas, but this has not yet been attempted very widely, and no information is available to model the geographical extent to which predictions apply. It is also clear that the factors influencing marine survival can dominate the accuracy of any predictive model for adults. Again there are considerable regional differences in the ranges of this variable. The causes appear to have their origins in the freshwater portion of the population model, in that smolt size, run size and timing of smolt runs all contribute to variation in marine survival.

To conclude, therefore, all the models we now have for salmon population dynamics must be treated as exactly that — dynamic models. Our interpretation of them depends on a fuller understanding of changes in the biotic and abiotic regulating mechanisms at differing stock levels, in different environments and over time. To answer the questions posed in the introduction — we are still a long way from understanding all the parameters regulating stock abundance in salmon or from a full assessment of the wider applicability of models obtained from index river data. There is a clear need for more long term data sets from a wide range of salmon rivers, and a constant appreciation of the dangers in applying the data from short time series in one river type too widely within the habitat range of the species.

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Comparison of Two Methods of Estimating Atlantic Salmon (*Salmo salar*) Wild Smolt Production

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Two methods to estimate wild smolt production of Atlantic salmon, *Salmo salar* L., were compared in the River Oir, a tributary of the River Sélune in Lower Normandy, France over 5 years. The first estimated smolt number by analysing the characteristics of the habitat and those of the juvenile salmon population in autumn. The second method estimated smolt number from trapping downstream migrants.

The study showed that 1+ smolts came mainly from the upper modal growth group of the 0+ autumnal population and the over winter survival rate depended on winter conditions, age-class, size and state of maturity. The comparison between the two methods showed that the 1+ and 2+ smolt number estimations could differ according to year and age-class. The two methods were in best agreement for the youngest age class (1+), the most abundant one in this study.

Different aspects are discussed to assess the reliability of the habitat method and to improve agreement between the two methods used.

Deux méthodes d'estimation de la production naturelle en saumoneaux de saumon atlantique (*Salmo salar* L.) sont comparées sur la rivière Oir, affluent de la Sélune (Basse-Normandie, France) durant 5 ans. La première estime le nombre de saumoneaux à partir des caractéristiques automnales de l'habitat et de la population de jeunes saumons. La seconde méthode évalue le nombre de saumoneaux à partir des captures faites par piégeage durant la dévalaison.

L'étude montre que les saumoneaux 1+ proviennent essentiellement du mode haut de la bimodalité observée en automne dans la population de 0+ et que le taux de survie hivernale dépend des conditions climatiques, de l'âge et de l'état de maturité. La comparaison entre les deux méthodes montre que les estimations du nombre de saumoneaux 1+ et 2+ peuvent différer selon l'année et l'âge. Les résultats obtenus apparaissent beaucoup plus proches pour la plus jeune classe d'âge (1+) qui est la plus abondante dans l'étude.

Différents aspects sont discutés pour connaître la fiabilité de la méthode à partir des caractéristiques automnaux de l'habitat et de la population de juvéniles et pour améliorer l'agrément entre les deux méthodes utilisées.

Introduction

A knowledge of smolt production is useful for the management of an Atlantic salmon (*Salmo salar* L.) population. There are two methods for estimating this production in French rivers, characterized by the presence of 1+ and 2+ age-classes in the smolt population (Prévost 1987). One is the trapping of juvenile salmon during downstream migration to the sea. It requires data on trapping efficiency in relation to water discharge conditions. The other method has been perfected by Baglinière and Champigneulle (1986). It is based on the characterization of the parr autumnal population in relation to habitat characteristics. The two methods have not previously been compared.

The establishment of an Atlantic salmon study program using a trap in the River Oir (a tributary of the River Sélune, Lower Normandy), has enabled comparison of these two methods for a 2-yr period (Baglinière et al. 1988). Analysis of these results showed a relatively good reliability of the method which used autumnal population characteristics. But it also demonstrated the need of further work in order to confirm certain hypotheses and to improve the precision of some parameters used in this method. Thus, after analysis of the characteristics of standing and migrating juvenile salmon populations in the River Oir, smolt numbers were estimated by both habitat and trapping methods and were compared over a 5-yr period.

Materials and Methods

Study Area (Fig. 1)

The study was carried out on the River Oir, a right bank tributary of the downstream part of the River Sélune in the Armorican Massif (Lower Normandy), from 1985 to 1990. The characteristics of the environment have been described by Baglinière et al. (1988). Briefly the River Sélune is 75 km long with a drainage area of 1010 km² and a mean slope of 1.9 ‰. It flows into The Channel in a common estuary with the River Sée. The Atlantic salmon production area is limited to the main river downstream of La Roche qui boit an impassable dam at 16 km from the sea, and two tributaries, the Rivers Beuvron and Oir. This last tributary is 19.5 km long with a drainage area of 85 km². The salmon production area is distributed over 12.3 km of the main-stem river and some tributaries, for example, Pont Levesque (5.4 km) and La Roche brook (3.4 km), between the trapping site and Buat watermill (impassable dam). The upstream and downstream traps are located at Cerisel Mill, 2.3 km before the confluence with the River Sélune (Fig. 2). Downstream trapping is not total except in conditions of low water discharge.

Characteristics o Habitat and Juvenile Populations

Habitats in the main-stem river were classified into four categories (Table 1) in July 1985, using the parameters proposed by Baglinière and Champigneulle (1986), namely, depth, velocity and substrate. The stretch was partitioned into four zones because of the non-uniform distribution of habitats categories in the main river (Z_1, Z_2, Z_3) and the necessity of taking La Roche brook into account (Z_4). Over the 2.25 km of the downstream water course of this tributary colonized by salmon, there is a fast run-riffles sequence with a rough substrate. Production surface area (riffle and runs of the river and La Roche Brook) was estimated at 44.982 m² (96.8% of the water surface area). This value may have decreased to 10% for the dry years of 1988 and 1989 .

The standing population was recorded by an electrofishing census (De Lury's method):

— in different sectors (62 to 666 m²) of the main river in October from 1985 to 1989.

— on the whole main-stem and in a small downstream sector (307 m²) of the La Roche Brook in October 1986.

— in several sectors of the La Roche Brook (23 to 224 m²) in October 1987 and on all the water course of this tributary colonized by salmon in October 1988, 1989 and May 1989.

Whichever capture (trapping and electrofishing) method was used, all fish were measured (fork length in mm) and scale samples taken from almost all juvenile salmon. Spermating males were detected by pressure on the flanks. The stage of juvenile migrating salmon (parr, presmolt, smolt) was defined according to morphology and the usual colour criteria (Johnston and Eales 1967).

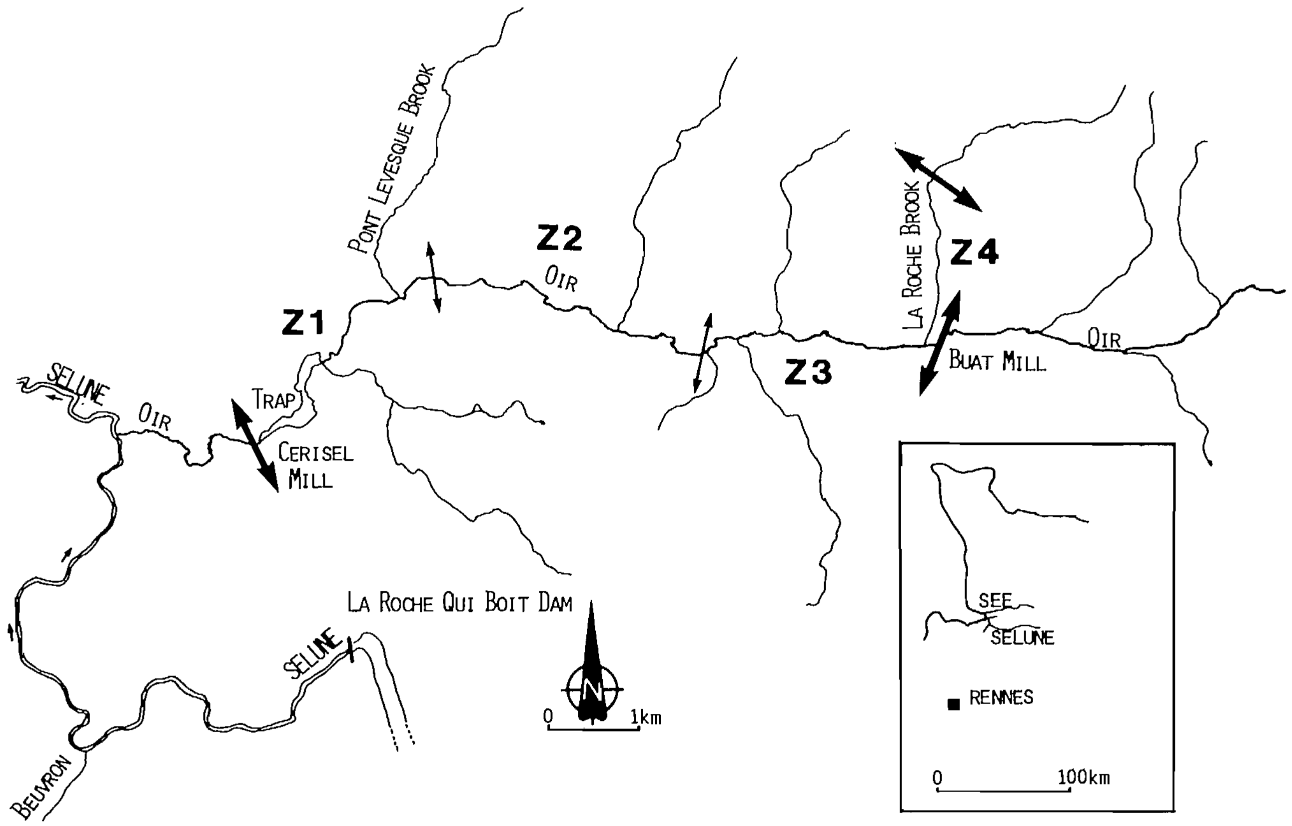

FIG. 1. The map of the River Oir and localization of four studied zones (Z_1, Z_2, Z_3 on the main river and Z_4 in La Roche Brook). ⟷ limit of study area ⟷ limit of zone

TABLE 1. Physical characteristics and water surface area of different habitat types in the R. Oir.

Type of habitat	Depth (cm)	Current Velocity(V) (cm/s)	Nature[2] of substrate	Aquatic vegetation	Percentage by zone: Zone 1 (4.4 km)	Zone 2 (4.7 km)	Zone 3 (3.2 km)	Water surface area: m^2	%
Riffle	< 25	> 40	Type 2 or 3	Present	24.2	20.7	52.5	13,878	32.7
Fast run	< 40	30< V <40	Type 2 or 3	Present	38.3	29.1	27.6	13,043	30.7
Slow run	> 40	20< V <30	Type 1, 2 or 3	Absent	32.0	47.2	17.1	14,061	33.1
Pool	> 60	< 20	Type 1, 2 or 3	Absent	5.5	3.0	2.8	1,483	3.5
TOTAL								42,465	100.0

[a] Nature of substrate was defined from three types: type 1 uniformly sandy; type 2: mixture of sand, gravels and pebbles (> 60% of fine materials cover the bottom surface); type 3: coarse (> 40% coarse materials (Ø > 2 cm) cover the bottom surface).

Estimation of Smolt Production

1. Baglinière and Champigneulle's Method (1986) (Habitat Method)

This method is based on three points:

a) Estimation of 0+ and 1+ parr autumnal density in sectors representative of different habitats in the main river and the brook. Pool habitat was neglected owing to the near absence of juveniles (Baglinière and Champigneulle 1982; Baglinière and Arribe-Moutounet 1985). Population densities were estimated by Seber and Le Cren's (1967) method and age structure was determined by scale reading (Baglinière 1979).

b) Analysis of autumnal size frequency distribution in 0+ parr. The existence of size bimodality was determined either using the Battacharya method (Laurent and Moreau 1973) or by direct observation of the size histogram in the field. To determine if 1+ smolts came from the upper mode as reported by Thorpe et al. (1980), 0+ salmon were marked differently according to size (1985 or 1987) or presence in one of the two modal groups.

c) Estimation of over winter survival rate in relation to size, age and state of maturity from capture-recapture experiments (tagging by either alcyan blue injection into the fin either fin-clipping or nasal microtag). Thus a mean value of the overwinter survival rate was calculated from:

— recapture of two age-classes of fish during either downstream migration (trapping) or subsequently (electrofishing census in May and October).

— value of the survival rate of 1+ parr between May and October (72.4%) in La Roche Brook in 1989.

The mean value obtained for each age-class has been increased by 5% to take into account the negative effects of handling and tagging on the survival of fish (Mears and Hatch 1976; Johnson and Ugedal 1988), tag loss (mainly with microtags) and incomplete data or recapture for certain years.

The estimated number of 1+ smolts produced by zone and by type of habitat data was expressed by the following equation (1) taking into account an overwinter survival rate in spermating fish half of that in immature fish (Myers 1984).

(1) $N = d \times A \times p \times s^{im}(1 - m/2)$ where

d = autumnal density of 0+ salmon (n/100 m^2)
A = surface area of the habitat (in 100 m^2)
} Parameters in relation to type of habitat

p = proportion of 0+ salmon in the upper mode
m = proportion of 0+ spermating in the upper mode
s^{im} = overwinter survival rate in immature fish
} Parameters in relation to zone

The same equation was applied to 1+ salmon for the estimation of 2+ smolts production. In this case, p was very close to 1, as the 2+ parr population recorded in autumn was very low (0 to 0.2%), and m was the proportion of spermating fish observed in the sample.

Total smolt production was estimated in three different ways:

— by adding the number of smolts produced by zone and by type of habitat (habitat cumulative method). As La Roche Brook was not electrofished in 1985, the density used in the estimation was that of the riffle habitat located in the main river near its confluence with the brook. Density in this riffle was always closest to that observed in the tributary in other years.

— by calculating the number of smolts produced in the whole main river from the mean values of the parameters and adding that estimated in La Roche Brook (whole basin method habitat).

— in using the estimation made from the total census of the River Oir and from the downstream part of the tributary in 1986 (total census).

2. *Smolt Trapping Method*

Trap efficiency was estimated each year from capture-recapture experiments made in different water discharge conditions. Tagged juvenile salmon were released at the same site above the trap every year (Fig. 2). The number of downstream migrants (from parr to smolt) was estimated by the following equation (2)

(2) $N = \Sigma N_i/e_i$ where

N_i = number of downstream migrants trapped during the time corresponding to the water discharge *i*
e_i = efficiency of the trap for water discharge *i*

In both methods, the smolt number was calculated in taking into account the confidence limits (95%) of density and each proportion (percentages of spermating fish and 0+ salmon in upper mode).

Data were analysed by standard statistical methods (χ^2, Student's *t*-test, analysis of variance, linear regression).

Results

Juvenile Population in Autumn

Population density varied, according to environment (brook, river), habitat, age-class and year from 0 to 39.1 *n*/100 m^2 (Table 2). The highest values were always observed in La Roche Brook and in the riffle habitat in the main river where 82% of the juvenile population was concentrated, on average, during the study period. Almost all the population was 0+ and 1+ year old, as 2+ fishes were present in the sample only in 1988 (0.2%) and 1989 (0.8%). In the main river, annual variation of the population density was twice-fold higher for 0+ salmon than for 1+ fish. In the tributary, this annual variation was similar for two age classes. Throughout the total study period, the 0+ population was the most abundant in the whole basin: 60 to 89% of total population in River Oir and 65 to 90% in the brook.

Mean fish size for the two age-classes depended strongly on zone ($p<0.01$, Table 3). It was largest in the downstream part of the main river (Z_1), and lowest in the tributary (Z_4) and similar in the two other zones. Annual variations, within zones, were smaller as significant differences were observed only in zones 3 and 4 for 0+ ($p<0.01$) and in zone 2 for 1+ ($p<0.02$). Nevertheless, for the total sample in the main river, the mean size of the two age-classes was higher in 1985 and 1988 (0+: $p<0.01$; 1+: $p<0.05$; Table 3).

Generally the 0+ salmon population showed a size bimodality in each zone of the main river but not in La Roche Brook (Z_4) from 1987 to 1989 (Table 3). The percentage of 0+ individuals in the upper mode and the difference between modal length changed according to zone and annual growth conditions. There was a significant correlation ($r=0.727$, $p<0.01$) between the percentage of upper mode individuals (p) and the mean fork length (Lf) of the 0+ population. A linear regression was calculated between those two parameters (3) $P = -0.9515 + 0.0157\ \text{Lf}$ ($n = 17$).

The proportion of 1+ spermating fish was high and generally greater than 50% (Table 4). On the other hand, the proportion of spermating 0+ salmon was much lower and varied greatly according to the year. Spermating fish of this age-class were always distributed in both modal growth groups.

Annual distribution of spermating fish changed according to zone (0+: $p<0.01$; 1+: $p<0.05$).

Migrating Juvenile Population (Table 5)

The number of salmon trapped over the entire study period ranged from 282 in 1987 to 888 in 1986. There was a balanced annual distribution of the two age-classes (1+ and 2+) in 1987 but a majority of 1+ fish in the other years. Mean size of 1+ salmon differed according to year ($p<0.01$) while mean 2+ fish size was higher only in 1986 ($p<0.01$).

Downstream migration took place between November 10th and May 15th, depending on the year,

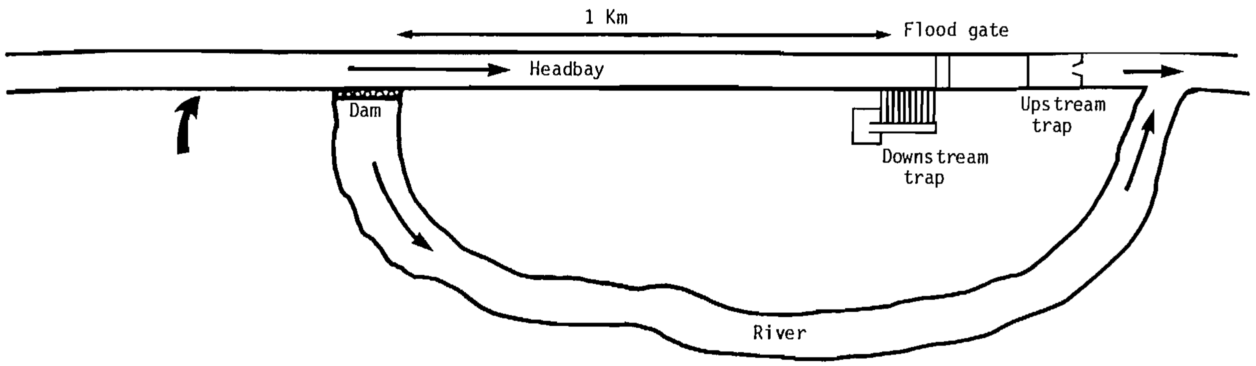

FIG. 2. Localization and scheme of the downstream trap. Release site of tagged juvenile salmon. ➜

TABLE 2. Juvenile salmon density (n/100 m^2 ±95% confidence limits) for each habitat type in the four zones of the River Oir.

			Density (n/100 m^2)									
			1985		1986		1987		1988		1989	
		Habitat	0+	1+	0+	1+	0+	1+	0+	1+	0+	1+
RIVER	Z_1	riffle	2.2(±0.0)	2.9(±0.0)	2.3(±0.0)	2.3(±0.0)	0.9(±0.0)	1.6(±0.0)	7.8(±1.3)	0.3(±0.0)	5.9(±0.2)	0.6(±0.0)
		run[a]	0.3(±0.0)	1.0(±0.0)	0.0(±0.0)	0.0(±0.0)	0.3(±0.0)	0.0(±0.0)	0.0(±0.0)	0.3(±0.0)	1.3(±0.0)	0.0(±0.0)
	Z_2	riffle	22.7(±0.5)	3.4(±0.0)	7.9(±0.8)	4.0(±0.0)	1.4(±0.0)	3.7(±0.0)	16.7(±0.2)	0.6(±0.0)	16.1(±0.4)	3.7(±0.2)
		run	8.4(±0.7)	0.1(±0.0)	2.6(±0.8)	1.4(±0.0)	0.0(±0.0)	0.0(±0.0)	6.2(±0.2)	0.0(±0.0)	5.6(±0.3)	0.7(±0.2)
	Z_3	riffle	12.3(±0.3)	0.5(±0.0)	2.8(±0.5)	1.9(±0.0)	6.8(±0.6)	1.7(±0.0)	11.7(±0.2)	2.4(±0.0)	23.8(±0.7)	1.9(±0.0)
		run	4.0(±0.4)	0.0(±0.0)	0.3(±0.0)	0.3(±0.0)	0.9(±0.0)	0.0(±0.0)	1.3(±0.0)	0.1(±0.0)	0.6(±0.0)	0.0(±0.0)
	Mean	riffle	12.3(±0.3)	1.6(±0.0)	3.8(±0.5)	2.4(±0.0)	3.1(±0.2)	2.3(±0.1)	12.1(±0.6)	1.1(±0.0)	15.1(±0.4)	2.1(±0.0)
		run	3.6(±0.4)	0.3(±0.0)	1.0(±0.3)	0.6(±0.0)	0.5(±0.0)	0.1(±0.0)	2.6(±0.1)	0.4(±0.0)	3.2(±0.1)	0.3(±0.0)
LA ROCHE BROOK	Z_4		23.5(±0.9)[b]	1.4(±0.0)[b]	10.4(±1.6)	5.0(±0.0)	27.3(±2.3)	2.6(±0.0)	18.5(±0.3)	7.9(±0.0)	39.1(±0.8)	4.8(±0.2)

[a] Run = fast run + slow run.

[b] Density observed in the riffle of the upstream part of the river near to the confluence with the brook.

TABLE 3. Mean fork lengths (Lf in mm) of juvenile salmon and the proportion of 0+ fish in the upper mode (*P* ±95% confidence limits) autumn in the River Oir from 1985 to 1989.

		1985			1986			1987			1988			1989		
	ZONE	Lf		*P*	Lf		*P*	Lf		*P*	Lf		*P*	Lf		*P*
		0+	1+		0+	1+		0+	1+		0+	1+		0+	1+	
RIVER	Z_1	108	161	63(±34)	101	151	86(±26)	100	168	75(±42)	104	159	76(±17)	103	161	59(±21)
		(7.7)[a]	(23.8)		(5.4)	(6.5)		(20.2)	(8.9)		(8.2)	(10.6)		(10.4)	(10.6)	
	Z_2	98	142	63(±10)	90	135	71(±15)	91	144	40(±43)	94	147	33(±11)	83	139	38(±11)
		(10.7)	(7.9)		(9.0)	(6.4)		(8.1)	(9.2)		(10.9)	(2.8)		(8.1)	(7.0)	
	Z_3	95	152	52(±08)	92	144	45(±17)	88	139	39(±18)	97	152	40(±15)	82	142	41(±11)
		(13.7)	(14.3)		(7.8)	(11.4)		(8.6)	(8.3)		(9.4)	(9.9)		(11.5)	(8.8)	
	MEAN	97	151	58(±06)	92	141	82(±09)	90	148	63(±16)	97	152	36(±08)	85	141	40(±08)
		(12.6)	(10.8)		(7.8)	(11.1)		(6.2)	(13.8)		(10.1	(9.4)		(12.0)	(9.6)	
LA ROCHE BROOK	Z_4				81	127	23(±17)	82	126	NO BIMO-	81	127	NO BIMO-	72	124	NO BIMO-
					(7.2)	(7.4)		(8.6)	(6.9)	DALITY	(11.8)	(7.4)	DALITY	(7.1)	(8.6)	DALITY
										34(±09)[b]			32(±04)[c]			18(±02)[c]
TOTAL CENSUS	Z_1 to Z_4				92	142	62(±02)									
					(10.7)	(12.1)										

[a] standard deviation

[b] *P* was estimated from a capture–recapture experiment made in relation to the size of 0+ fish in autumn.

[c] *P* was calculated from the equation (3) (see text).

TABLE 4. Percentage (% ± 95% confidence limits) of sampled juvenile salmon wich were spermating at the beginning of October in the River Oir from 1985 to 1989.

	Zone	Age Class														
		0+										1+				
		1985		1986		1987		1988		1989		1985	1986	1987	1988	1989
		%[a]	m[b]	%	m	%	m	%	m	%	m	%[a]	%	%	%	%
RIVER	Z_1	0	0	0	0	50(±50)	67(±53)	36(±19)	47(±22)	18(±16)	15(±20)	75(±24)	57(±37)	60(±43)	100(±0)	100(±0)
	Z_2	18(±07)	24(±10)	8(±09)	7(±10)	0	0	34(±11)	33(±19)	01(±03)	00(±00)	54(±27)	39(±20)	86(±19)	0(±0)	53(±26)
	Z_3	13(±06)	14(±08)	15(±12)	19(±20)	0	0	23(±13)	18(±18)	14(±08)	06(±09)	17(±36)	60(±19)	83(±30)	27(±27)	33(±39)
	MEAN	15(±04)	18(±06)	10(±07)	11(±08)	05(±07)	13(±17)	31(±08)	35(±13)	09(±04)	09(±07)	55(±18)	51(±13)	79(±17)	33(±24)	52(±21)
LA ROCHE BROOK	Z_4	—	—	12(±13)	0	07(±05)	15(±11)	08(±02)	08(±04)[c]	03(±01)	05(±03)[c]	—	80(±21)	59(±24)	57(±06)	61(±08)
TOTAL CENSUS	Z_1 to Z_4	—	—	07(±01)	07(±01)	—							52(±01)			

[a] Proportion of spermating fish in the total population sampled by zone or on the whole main river. For 1+ individuals, this proportion corresponds to m defined in the estimation equation of the 2+ smolts number.

[b] Proportion of 0+ spermating salmon in the upper mode.

[c] Calculated factor after to have estimated the proportion (p) from the equation (3).

TABLE 5. Number (N) and characteristics of migrating juvenile salmon caught by trapping in the River Oir from 1986 to 1990.

		Stage (% of total)			1+ individuals				2+ individuals			
Year	Period of migration	parr	presmolt	smolt	median date of migration [a]	N	%	mean length (mm)	median date of migration [a]	N	%	mean length (mm)
1986	3/01–15/05	42.8	15.4	41.8	21/04	849	95.9	130(08.9)[b]	28/03	39	4.1	161(10.3)
1987	14/02–30/04	5.0	31.8	63.2	15/04	148	52.5	126(09.6)	6/04	134	47.5	154(11.2)
1988	10/11–05/05	3.4	53.6	43.0	12/04	280	91.2	130(10.6)	29/03	27	8.8	154(15.7)
1989	21/11–08/05	2.3	54.2	43.5	13/04	492	89.1	134(15.8)	29/03	60	10.9	152(10.5)
1990	27/01–08/05	0.6	46.5	52.9	14/04	707	94.9	132(09.8)	31/03	38	5.1	154(12.8)

[a] date corresponding to the capture of 50 % migrating juvenile for each age class.

[b] standard deviation.

but most fish (75 to 82%) migrated in April. The timing of migration was similar and earlier in the four latter years (median date between the 9th and 14th April) than in 1986 (mean date 21st April). Each year, the parr migrated first, then came the presmolts and lastly the smolts. However, the distribution of the different stages in the migrating juvenile population was different according to year ($p<0.01$) owing to a large proportion of smolt in 1987 and a equal number of parr and smolt in 1986. The 2+ fish always migrated, on average, before the 1+ ones.

Estimation of Smolt Production

Origin of 1+ Smolt (Table 6)

From the analysis of 0+ salmon tagged in autumn and recaptured as 1+ presmolt or smolt the next spring, we could see that:

— in each year, 1+ smolt came significatively more from the upper mode 0+ ($p<0.01$).

— the very high percentage of 1+ smolt coming from the upper mode 0+ autumnal population (89 to 100%) allowed the proportion of 0+ salmon in the upper mode to be taken into account (p) (direct observation, estimation by the Battacharya method or from the equation (3) when growth bimodality was not present) for estimating the 1+ smolt number.

TABLE 6. Number of 0+ salmon tagged in autumn according to size and recaptured as 1+ presmolts or smolts during downstream migration.

Year	0+ salmon		
	Caught in autumn		recaptured as 1+ presmolt or smolt
	type	number	
1985	Lf≥90	178	55
	Lf<90	78	3
1986	Upper mode	246	89
	Lower mode	151	11
1987	Lf≥80	74	24
	Lf<80	46	0

Estimation of the Overwinter Survival Rate (Table 7)

Analysis of the minimum and maximum values of the overwinter survival rates showed that:

— 0+ fish had better survivals rate than did 1+ fish.

— there were large annual variations. 0+ salmon survival was similar for the winters of 1986 and of 1987 (very cold in February and January: it means 3 weeks of very low air temperature between −10° and −20°C) but much lower than the other winters (mild conditions: it means no air temperature below −5° C) ($p<0.001$). 1+ parr survival was similar in the winters 1987 to 1989 but higher the winter of 1990 ($p<0.01$).

— survival in spermating fishes was lower than in immature ones only in winter 1989 for 0+ salmon (data for 1 year) and in winter 1990 for 1+ fish (data for 2 years).

From the data, mean overwinter survival rate of upper mode 0+ salmon could be estimated at 41% (36 + 5 (negative effect of handling)) in cold winters (1986 and 1987) and at 63% (58 + 5) in mild winters (1988 to 1989). The same value was used for the winter of 1990 very similar to the previous one. For 1+ fish, it was estimated at 32% (27 + 5) whatever the year.

Efficiency of Trapping

Efficiency of trapping varied from 40 to 100% according to water discharge conditions. It was much higher in period of low and mean water level (65 – 100%) than in period of spate (40 – 52%). No efficiency variability could be observed in relation to size and age of juvenile salmon since all the released fish were one year old with a fork length between 13 and 15 cm.

Comparison Between the Two Estimation Methods (Table 8).

There was a significant linear regression calculated between the 1+ smolt number estimated from trapping (x) and from two habitat methods (y):

habitat cumulative by zone:

(4) $y = 213.6(\pm 483.6) + 0.647(\pm 0.627)\,x \quad r = 0.884 \quad p < 0.05$

habitat on whole basin:

(5) $y = 206.6(\pm 354.8) + 0.558(\pm 0.458)\,x \quad r = 0.913 \quad p < 0.05$

Futhermore theses equations differed not significantly from this of type: $y = x$.

Thus, 1+ smolt numbers estimated from the habitat method were not significantly different from those obtained from trapping. Nevertheless there was a greater error associated with estimations from habitat method for 1+ fish since the relative errors ranged from 18 to 47% (they were higher for habitat method by zone (25–47%) than for whole basin habitat (18–43%)).

There was no significant correlation ($p > 0.05$) between the 2+ smolt estimates obtained from the two methods. Futhermore 2+ smolt number estimated from the habitat method were significantly ($p < 0.05$) higher than that evaluated by trapping except for 1987.

Discussion

Smolt number estimates from the two methods differed according to year and age-class with results obtained for 1+ smolts in closest agreement but those given by the trapping method were more precise.

TABLE 7. Over winter survival rate calculated from recapture data in 0+and 1+ salmon.

		Tagged fish in autumn		Over winter survival rate (%)	
Age	Winter	Type	Number	Minimum	Maximum
0+	1986	0+ total	256	27.5	37.3
		0+ upper mode	178	28.7	38.5
		0+ low mode	78	25.0	34.6
	1987	0+ total	397	≥ 25.4	≤ 36.7
		0+ upper mode	246	≥ 30.5	≤ 44.8
		0+ low mode	151	≥ 15.9	≤ 22.3
	1988	0+total	157	≥ 45.1	≤ 64.3
		0+ upper mode	90	≥ 49.3	≤ 70.0
		0+ low mode	67	≥ 38.6	≤ 54.2
	1989[a]	0+ total	559	48.1	56.7
		0+ non spermating	513	50.9	60.6
		0+ spermating	46	14.1	16.3
1+	1987	1+ total	379	23.0	33.3
	1988	1+ total	41	14.6	29.3
		1+ non spermating	12	16.7	33.3
		1+ spermating	29	13.8	27.6
	1989	1+ total	281	22.1	29.2
	1990	1+ total	148	≥ 8.8	≤ 10.1
		1+ non spermating	57	≥ 14.0	≤ 17.5
		1+ spermating	91	≥ 2.2	≤ 2.2

[a] In 1989 the tagging of 0+ salmon was made only in relation to state of maturity.

Different aspects are discussed in order to assess the reliability of the habitat method, to increase its precision and to improve its agreement with the trapping method (large confidence limits of agreement in relation to the short period of data recording (5 years).

Origin of 1+ Smolts

This study has verified the hypothesis that, in wild conditions, most upper mode 0+ salmon become smolt the following spring, corroborating results obtained in a previous study (Baglinière and al. 1988). However, the recapture during downstream migration of 1+ fish tagged when small or as lower mode 0+ salmon implies a small proportion of these fish contribute to 1+ smolt production. Nevertheless, the similar 1+ smolt estimations from the two methods enabled us to consider the proportion of 0+ salmon in the autumnal upper mode (p) as a reliable parameter for the production equation of the 1+ smolt.

Electrofished Surface Area, Representative Sectors and Number of Sampled Fish

The percentage of water surface area sampled was low (4.4. and 6.1%), but similar to that sampled in Girnock Burn in Scotland (7%: Buck and Hay 1984) and greater than that studied in the River Scorff (2.1%: Baglinière and Champigneulle 1986). Run habitats and particularly the slow runs were undersampled compared to riffles in 1985 and 1986, while its significance in the water surface area was 66% of the whole basin and 76% in Zone 2, but salmon density was always very low. During these 2 years, La Roche Brook was not well sampled as there was no electrofishing census in 1985 and only one in a small downstream sector in 1986. These considerations could explain the larger differences observed between the 1+ and 2+ smolt number estimations from both methods in 1986 and 1987.

From 1987, test sectors were more representative of the whole basin with more homogeneous recordings carried out in relation to the different habitat categories of each main river zone (notably in distinguishing overall the two run types defined in Table 1) and taking into account the total La Roche Brook area colonized by salmon. This brook produced 25% of the total smolt population in the whole basin (Charlot 1989).

As a result of the above changes, 1+ smolt number estimates from both methods were closer, while

TABLE 8. Estimation of Atlantic salmon smolt production (± 95% confidence limits) in the R. Oir from 1986 to 1990.

Year of trapping	Method		Estimated number of smolts		
			1+	2+	Total
1986	Habitat	Cumulative by zone	921(±235)	82(±14)	1003(±249)
		Whole basin	854(±156)	86(±11)	940(±167)
	Trapping		1270(±181)	55(± 8)	1325(±189)
1987	Habitat	Cumulative by zone	290(±111)	180(±32)	470(±143)
		Whole basin	306(±111)	157(±16)	463(±127)
	Total census		164(± 35)	129(± 7)	293(± 42)
	Trapping		199(± 37)	180(±33)	379(± 70)
1988	Habitat	Cumulative by zone	406(±192)	84(±16)	490(±208)
		Whole basin	372(±161)	100(±15)	472(±176)
	Trapping		408(± 62)	46(±10)	454(± 72)
1989	Habitat	Cumulative by zone	707(±293)	147(±13)	854(±306)
		Whole basin	588(±179)	135(±12)	723(±191)
	Trapping		761(±127)	97(±15)	858(±141)
1990	Habitat	Cumulative by zone	954(±294)	127(±22)	1081(±316)
		Whole basin	818(±196)	119(±16)	937(±212)
	Trapping		776(± 69)	41(± 4)	817(± 73)

those of 2+ smolts remained different. The small size of the River Oir did not always enable the determination of a large homogeneous habitat, owing to a mosaic distribution of habitats. This aspect involved two consequences. First it could modify, in years of very low density, the expression of habitat requirements of 0+ and 1+ salmon, on which the method of Baglinière and Champigneulle (1986) was grounded. That could explain, partly, the large differences between the estimates of 2+ smolts, as 1+ parr densities were often very low in autumn. Then this aspect implied to make electrofishing census in small sectors in order that they are representative of different habitats leading generally to the capture of a small number of juvenile salmon. Nevertheless, for increasing the precision of the habitat method, it is necessary to catch a large number of fish in order to decrease the confidence limits of the different proportions used in the equation (1). Precision of the habitat method will mainly be improve under that condition and not in increasing the surface area of electrofished sectors or the efficiency of electrofishing that always was high (70–100%).

Overwinter Survival

The overwinter survival rate of 0+ salmon seemed typical. The value estimated in mild winters (63%) was very close to that calculated by Baglinière and Champigneulle (1989) and used by Baglinière et al. (1988). The overwinter survival of 0+ salmon decreased when winter severeness increased. In such conditions mid-winter could be stressfull (Cunjak 1988). Survival of 0+ salmon also seemed to depend on the autumnal size, as mortality was higher in lower mode 0+ salmon than in upper mode fish as observed by Pickering and Pottinger (1988) under artificial conditions.

Overwinter survival of 1+ salmon appeared much less than expected and possibly underestimated. The obtained value (32%) was much lower than that estimated by Baglinière and Champigneulle (1986) (80%). Unlike 0+ salmon, apparently overwinter survival did not change according to year and climatic conditions. The lowest value observed (1990) could have resulted from tagging by multiple fin clipping leading to a decrease of survival as reported by Johnsen and Ugedal (1988). The lower overwinter survival of 1+ salmon, compared to that of 0+ fish, may be related to the influence of precocious male sexual maturity since the percentage of spermating fish was much higher in 1+ salmon than in 0+ fish and the precocious sexual maturity resulted in a large mortality rate (Osterdahl 1969; Leyzerovich 1973; Dalley and al. 1983; Myers 1984; Hansen and al. 1989). Overwinter survival was twice as high (17%) in 1+ immature fish as in mature ones (7%). The true influence of precocious sexual maturity on the overwinter survival of juvenile salmon, however, is uncertain as the censuses were made at the beginning of October, resulting in an underestimate of the number of 0+ and 1+ spermating fish (salmon usually spawn in mid-December).

Trapping Efficiency

Capture-recapture experiments were performed totally with 1+ fish during the month of April, corresponding to the migration peak of this age-class. In 1986 and 1988 no sampling was carried out between the end of March and the beginning of April during the flood period, corresponding to the migration peak of 2+ smolts always earlier than that of 1+ smolts (Baglinière 1976). From these different considerations it is probable that the 2+ smolt number trapping estimates were underestimated.

Influence of Climatic Conditions on Stage at Migration

Many fish (up to 43% in 1986) migrated as parr stage. In Girnock Burn, Buck and Hay (1984) did not observe completely smoltified salmon during the spring migration. Futhermore, tagged parr migrating in autumn were recaptured in this stream as grilse or multi sea-winter salmon (Youngson et al. 1983). The low 1+ smolt number estimate from the habitat method versus trapping in 1986 could be due to the high proportion of migrating parr. Lastly, Duston et al. (1991) showed that an increase in freshwater temperature during the period of downstream migration could accelerate the loss of smolt characteristics. In 1990, the water temperature during seaward migration (end of February–beginning of May) was between 3 to 5°C higher than for previous years, which might account for the smaller proportion of trapped 1+ smolts that year as compared to the habitat estimates.

Conclusion

This study shows that further work was necessary to improve the agreement between the two methods of estimation of smolt production and the precision of habitat method. For this one, the accuracy of the estimation depends directly on (1) the quality of the representation of the test sectors studied in each zone, (2) the density and the number of juvenile salmon sampled which must be large in order to decrease the confidence limits of the different parameters used in the equation of smolt number. Thus the habitat method would seem more difficult to use in streams with a low level of salmon population, (3) the necessity to analyse all the environmental (water temperature and discharge, habitat) and biotic factors (precocious sexual maturity, age, density) influencing the overwinter survival of fish.

In the trapping method, it is necessary to improve the efficiency of the trap in relation to water discharge and temperature, age and physiological state.

Nevertheless, this study demonstrates that the estimation method of smolt production from the autumnal characteristics of the habitat and the juvenile salmon population is an available tool and could be useful for the rational management of Atlantic salmon stocks even if there are some disadvantages (1) large confidence limits of the estimated number (up to 50%) and (2) overestimation of 2+ smolt production.

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An Extrapolation of the Potential Emigration of Atlantic Salmon (*Salmo salar*) Smolts from Newfoundland Lakes in the Absence of Brook Trout (*Salvelinus fontinalis*)

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RYAN, P. M. 1993. An extrapolation of the potential emigration of Atlantic salmon (*Salmo salar*) smolts from Newfoundland lakes in the absence of brook trout (*Salvelinus fontinalis*), p. 203–207. *In* R. J. Gibson and R. E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

The calculated annual smolt emigration of 3.2–26.7 smolts · ha^{-1}(Sm) from two small Newfoundland lakes with a water quality typical of Newfoundland's fresh waters was related to the density (number · ha^{-1}) of salmon in the lakes in the spring (Sp) over a 5-yr period by: Sm = 0.83Sp – 9.22; r = 0.987. A relationship between the average annual density (number · ha^{-1}) of trout (Ta) and the average annual density of salmon (Sa) in the lakes, Ta = 62.59–1.09 Sa; r = 0.897, was used to calculate a theoretical maximum salmon density in the spring of 90.3 salmon · ha^{-1} in the absence of trout. The theoretical maximum smolt emigration at this theoretical maximum spring density was calculated as 65.7 smolts · ha^{-1} · yr^{-1}. The calculated average annual smolt migration rate of 13.4 smolts . ha^{-1} from the study lakes, if applied to all standing waters accessible to salmon in insular Newfoundland, would result in 7.2 million smolts · yr^{-1}. The theoretical maximum smolt migration rate from the study lakes could result in 35.1 million smolts · yr^{-1} from accessible Newfoundland standing waters, far in excess of estimated current smolt production.

L'émigration annuelle calculée de smolts (3,2–26,7 smolts · ha^{-1} (Sm)) de deux petits lacs de Terre-Neuve présentant une qualité de l'eau typique des eaux douces terre-neuviennes a été mise en rapport avec la densité (nombre · ha^{-1}) de saumons dans les lacs au printemps (Sp) sur une période de 5 ans de la façon suivante : Sm = 0,83Sp - 9,22; r = 0,987. On s'est servi de la relation entre la densité annuelle moyenne (nombre · ha^{-1}) de truites (Ta) et la densité annuelle moyenne de saumons (Sa) dans les lacs, Ta = 62,59–1,09 Sa; r = 0,897, pour obtenir par calcul une densité maximale théorique au printemps de 90,3 saumons · ha^{-1} en l'absence de truites. On a calculé que les migrations théoriques maximales de smolts à cette densité théorique maximale du printemps étaient de 65,7 smolts · ha^{-1} · an^{-1}. Le taux annuel moyen calculé de migration des smolts (13,4 smolts · ha^{-1}) des lacs d'étude, si on l'appliquait à toutes les eaux dormantes accessibles aux saumons dans l'île de Terre-Neuve, donnerait un résultat de 7,2 millions de smolts · an^{-1}. Le taux théorique maximum de migration des smolts des lacs d'étude pourrait donner un résultat de 35,1 millions de smolts · an^{-1} provenant des eaux dormantes accessibles de Terre-Neuve, ce qui dépasse fortement l'estimation de la production actuelle de smolts.

Introduction

Knowledge of the potential of individual river systems and their component habitats to produce Atlantic salmon smolts is a requirement in setting catch quotas so that sufficient adults can escape to spawn. Additionally, knowledge of this smolt potential is a requirement for the recognition of environmental stresses such as acid precipitation (Watt et al. 1983; Gunn 1986).

In insular Newfoundland, riverine portions of Atlantic salmon river systems are estimated to produce 2.8–8.9 million smolts · yr^{-1} (Pippy 1982). However, an unknown smolt production occurs naturally in Newfoundland's abundant lakes (Pepper 1976; Chadwick and Green 1985; Ryan 1986a; O'Connell and Ash 1989). Lakes cover over 10% of the island's land mass (Whelan and Wiseman 1975).

A large part of the variation in lacustrine smolt production rate among river systems is thought to be due to interactions with potential competitors and predators (O'Connell and Ash 1989). Rose (1986) reviewed the strong evidence that environmentally mediated interactions determine the varying proportions of each similar salmonid in a total potential salmonid biomass within individual systems.

In this paper, the potential contribution of the smolt migration from Newfoundland lakes to the total annual smolt migration is estimated using data on the population dynamics of Atlantic salmon and brook trout in two Newfoundland lakes. This estimated potential and the relationships upon which it is based may serve in subsequent determinations of Atlantic salmon smolt production in lakes and in river systems in their entirety.

Methods

Study Area

Headwater and Spruce ponds are dilute (mean conductance 35 *m*S $\cdot$cm^{-1}), brown-water lakes within the Department of Fisheries and Oceans' Experimental Ponds Area at the headwaters of the Gander River system (Ryan and Wakeham 1984). Their physical and chemical characteristics approximate the average descriptors of water quality in insular Newfoundland (Ryan and Wakeham 1984; Ryan et al. 1990). Headwater Pond (76.1 ha, maximum depth = 3.3 m, mean depth = 1.1 m) drains 3.5 km to the north into Spruce Pond (36.5 ha, maximum depth = 2.1 m, mean depth = 1.0 m) and the Spruce Pond outlet flows about 155 km northeast to the Atlantic Ocean. The closest major concentration of salmon spawning substrate is about 12 km downstream of Spruce Pond (Traverse 1972; Ryan and Wakeham 1984). In addition to anadromous Atlantic salmon, other fishes present in the lakes are the brook trout (*Salvelinus fontinalis*), the American eel (*Anguilla rostrata*), and the threespine stickleback (*Gasterosteus aculeatus*).

Smolt Migrations

Atlantic salmon and brook trout were censused for density, biomass, and age composition each spring and fall from 1978–83 in Spruce Pond and from 1979–83 in Headwater Pond using fyke nets and Schnabel multiple mark–recapture techniques as detailed in Ryan (1984, 1990). The number of salmon smolts migrating out of the lakes each year has been calculated as the loss in numbers of salmon from each of the age groups over the spring-to-fall period (Ryan 1986a). The calculated number of smolts has been related to the number of salmon present in the lakes in the spring of the same year by least-squares regression (Dixon and Massey 1969) to obtain a predictor of the smolt migration at given spring salmon densities (Ryan 1986b). In this paper, both lakes are considered as a single entity of 112.6 ha over the period 1979–83 to compensate for the interlake movements which occur (Ryan 1986a).

In order to estimate the maximum potential smolt migration from the study lakes, I assumed that Rose's (1986) hypothesis of a reciprocal salmonid abundance is valid and that no brook trout were present in the lakes. I employed density, rather than biomass, as the measure of abundance for convenience, since smolt counts are typically reported as numbers rather than weights. Mean lengths of salmon and trout in the study lakes were similar (152 and 171 mm, respectively) but mean weights differed substantially (44 and 75 g, respectively) (Ryan 1990). The maximum average annual salmon density was calculated from the inverse relationship between average annual trout density and average annual salmon density. This density estimate was used to calculate the theoretical maximum spring salmon density in the absence of trout which was in turn used to estimate the theoretical maximum smolt emigration at that density.

The calculated smolt migrations from the study lakes under actual conditions and in the theoretical absence of brook trout, expressed on an areal basis, were applied to the estimates of standing waters available in order to extrapolate the potential emigration of Atlantic salmon smolts from all insular Newfoundland lakes.

Results

The calculated smolt migration rate from Headwater and Spruce ponds, 1979–83, averaged 13.4 smolts · ha^{-1} · yr^{-1}, ranged from 3.2 to 26.7 smolts ha^{-1} · yr^{-1}, and was a significant ($p < 0.05$) correlate of spring salmon density in the lakes over the range of 14.2–42.8 salmon · ha^{-1} (Fig. 1). Residual salmon were always present in the lakes in the fall after the smolt run and these fish tended to be proportionately less at higher stock densities.

Over the range of densities encountered in the study lakes, average annual trout density was a significant ($p < 0.05$) inverse correlate of average annual salmon density (Fig. 2). This relationship was consistent with Rose's (1986) hypothesis of a reciprocal abundance of similar salmonids. In the absence of trout, average annual salmon density (Sa) estimated from the relationship is:

$$\mathrm{Sa} = \frac{62.59}{1.09} = 57.42 \text{ salmon} \cdot \text{ha}^{-1}$$

Thus, average annual salmon density in the absence of trout would be given by:

$$\frac{\text{Spring density} + \text{Residual fall density}}{2} = 57.42 \text{ salmon} \cdot \text{ha}^{-1}$$

or;

$$\text{Spring density} + \text{Residual fall density} = 114.84 \text{ salmon} \cdot \text{ha}^{-1}$$

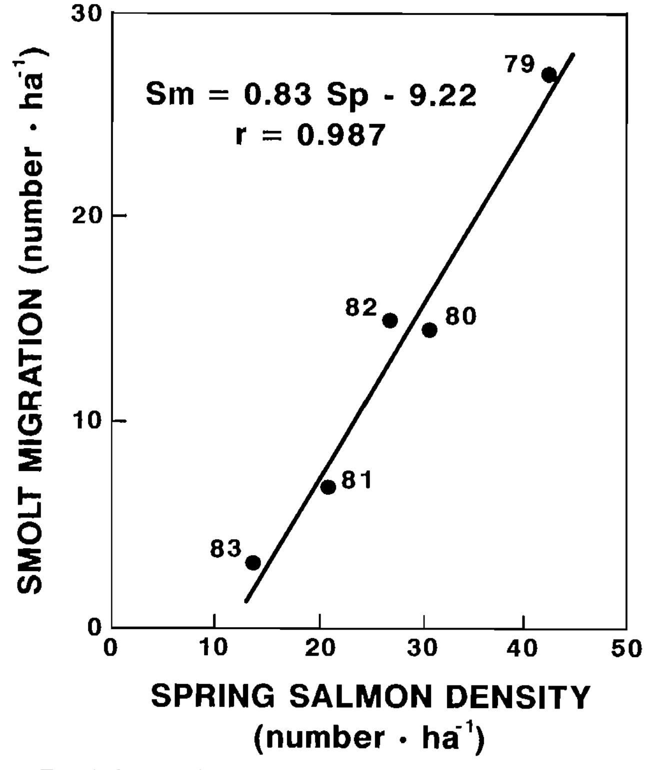

FIG. 1. Smolt migrations (Sm) from the study lakes related to the spring densities (Sp) of salmon in the lakes in the same year. Years of census are indicated. Redrawn from Ryan (1986b).

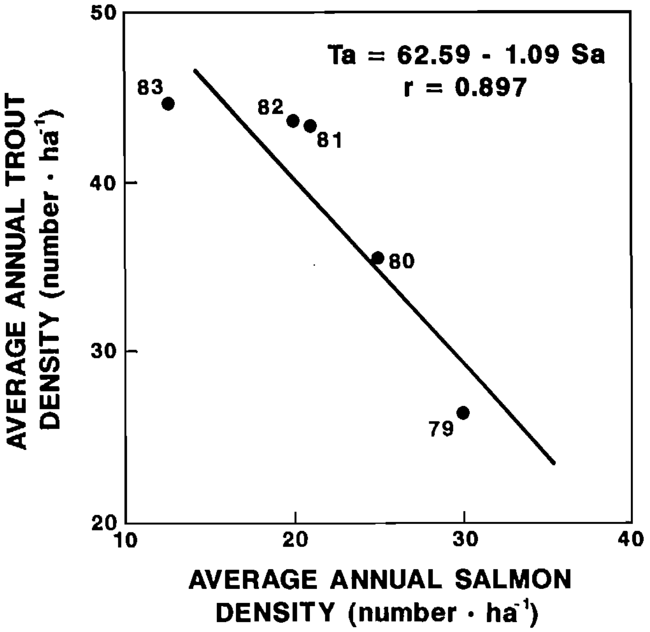

FIG. 2. Average annual trout (Ta) densities $\frac{\text{(spring density + fall density)}}{2}$ related to average annual salmon (Sa) densities in the study lakes. Years of census are indicated. Data are available in Ryan (1990).

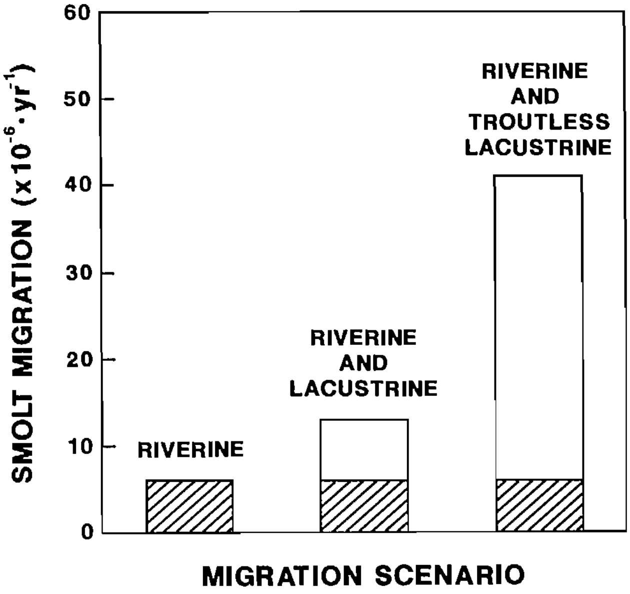

FIG. 3. Estimated annual insular Newfoundland smolt migration from riverine areas (midpoint of range of Pippy 1982), riverine and lacustrine (present study average) areas, and riverine and troutless lacustrine (present study theoretical maximum) areas.

Since the residual fall density is equal to the spring density minus the smolt density and smolt density (smolts · ha^{-1}) equals:

$$Sm = 0.83Sp - 9.22 \text{ (Fig. 1)},$$

then, by substitution, the theoretical maximum spring density (Sp) can be obtained from:

$$Sp + (Sp - Sm) = 114.84 \text{ salmon} \cdot \text{ha}^{-1} \text{ or;}$$
$$Sp = 90.27 \text{ salmon} \cdot \text{ha}^{-1}$$

TABLE 1. Calculated Atlantic salmon smolt migrations from the study lakes and insular Newfoundland lakes at smolt densities estimated from the study lakes, 1979–83, and at extrapolated theoretical maximum densities in the absence of brook trout.

Scenario	Smolt density (no. · ha^{-1})	Number of smolts
Headwater and Spruce ponds, 1979–83 average.	13.4	1,509
Headwater and Spruce ponds, theoretical maximum (no trout).	65.7	7,398
Insular Newfoundland lakes at current study average.	13.4	7,162,997
Insular Newfoundland lakes theoretical maximum (no trout).	65.7	35,120,066

At a maximum spring density of 90.27 salmon · ha^{-1}, the estimated smolt migration rate (Fig. 1) would be 65.70 smolts · ha^{-1}, leaving a fall population of 24.57 salmon · ha^{-1}, and resulting in an average annual density of 57.42 salmon · ha^{-1}.

Atlantic salmon river systems in insular Newfoundland have a drainage area of 77,871.24 km^2 and the riverine areas of these systems produce an estimated 2.9–8.9 million smolts · yr^{-1} (Pippy 1982)[1]. About 10% of the drainage area of these rivers, or 7,942.8 km^2, is made up of standing waters with surface areas of 0.405 ha or greater (Whelan and Wiseman 1975). If 67.3% of this standing water were accessible to salmon, as is estimated for the riverine parr rearing areas (Anon. 1978), accessible standing waters would constitute 5,345.52 km^2 of the drainage basins of insular Newfoundland's salmon rivers. At the calculated average annual smolt emigration rate of 13.4 smolts · ha^{-1} from standing waters in the Experimental Ponds Area, the calculated accessible standing waters in Newfoundland's salmon rivers would have a smolt emigration of 7.2 million smolts · yr^{-1} (Table 1). At the estimated theoretical maximum smolt emigration rate of 65.7 smolts · ha^{-1} · yr^{-1}, insular Newfoundland's accessible standing waters would have a smolt emigration of 35.1 million smolts · yr^{-1}, far in excess of estimated riverine production (Table 1).

The addition of lacustrine smolt migrations from current study averages to estimated riverine smolt production (Fig. 3) suggests a possible doubling of insular Newfoundland smolt production estimates. Similarly, the addition of theoretical smolt migrations from possible troutless lakes to estimated riverine smolt production (Fig. 3) suggests an even higher theoretical smolt production potential.

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[1] Calculated from a total estimated smolt production of 37.3–114.6 smolts · yr^{-1} · km^{-2} of drainage basin and an estimated 1.3–4.0 smolts · yr^{-1} · 83.6 m^{-2} from accessible river (stream) area with gravel, boulder, or rubble substrate (Pippy 1982).

Discussion

There are a number of factors which have affected the precision of the estimates of smolt emigration. These include the approximation of census requirements, an unknown mortality rate of parr, and the migration of precocious parr between spring and fall censuses. However, as discussed by Ryan (1986a, 1990), these factors have not precluded the application of the estimates for practical purposes.

The estimates of smolt migration rate from the study lakes are estimates of lacustrine smolt emigration rate rather than lacustrine production as a result of the use by young salmon of both lake and river environments. In the study lakes, the first lakeward migrations of salmon from streams occurs after the second year of life. Some of these fish may return to the streams for varying periods prior to smoltification in the lakes (Ryan 1986a). This pattern of lake use by salmon appears to be a common one in insular Newfoundland (Pepper 1976; Hutchings 1986), although in some areas of the island lake use may occur earlier (O'Connell and Ash 1989).

The annual variation in smolt migration rates from the study lakes, 3.2–26.7 smolts $\cdot$ ha^{-1}, appears to be representative of values of lacustrine smolt production calculated for Newfoundland waters. In two other river systems comprised of 96 and 98% lake habitat, annual lacustrine smolt production was estimated as 10.1 smolts $\cdot$ ha^{-1} (96% of the total) (O'Connell and Ash 1989) and 15.0 smolts $\cdot$ ha^{-1} (67% of the total) (Chadwick and Green 1985), respectively.

It seems probable that the proportion of naturally occurring lacustrine smolt production in watersheds is a function of the proportion of lacustrine habitat available and the degree of inter- and intraspecific competition, both in fluvial and lacustrine habitats as hypothesized by Pepper (1976), Chadwick and Green (1985), Pepper et al. (1985), and O'Connell and Ash (1989).

If the estimated average annual smolt migration from the study lakes is representative of standing waters in Newfoundland's salmon river systems, the corresponding calculated value of 7.2 million smolts $\cdot$ yr^{-1} from insular Newfoundland lakes (Table 1) suggests that lacustrine smolt emigration at least approaches the estimated riverine production of 2.9–8.9 million smolts $\cdot$ yr^{-1} (Pippy 1982) in insular Newfoundland. Furthermore, as supported by the results of the present study, it appears true that lake use by Atlantic salmon is a function of competition and predation mediated by environmental factors. Thus, variations in brook trout abundance in lakes might be expected to result in a varied lake use by salmon and in further variations in Newfoundland smolt production potential. Accordingly, estimates of potential Atlantic salmon production should take into account the abundance and production of other similar salmonids.

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Egg-to-Smolt Survival and Fry-to-Smolt Density Dependence of Keogh River Steelhead Trout

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The population dynamics of steelhead trout (*Oncorhynchus mykiss*) in a coastal stream on Vancouver Island, B.C., were studied since 1976. Estimates of numbers of spawners, fecundity, potential egg deposition (n = 12 yrs), fry abundance (n = 7 yrs) and parr abundance (n = 2 yrs) provided information on survivorship when combined with smolt counts from brood years. The relationship between eggs and fry (1-month post-emergence) was linear with the exception of 1976, when flows during spring were exceptionally high. Mean egg-to-fry survival was 6.5% (min., 1.8%; max., 11.5%). Mean fry-to-smolt survival was 12.9% (min. 3.3%, max. 21.9%). The relationship between fry and smolts suggested an asymptotic yield of ca. 7,500 smolts, or 2.7 smolts per 100 m^2 of river, based on a Beverton-Holt recruitment relationship. Yield of smolts by brood year varied from 5,725 to 10,750 fish. Variation was larger in the annual yield of smolts, which was comprised of four age-classes; 2,104 (1978) to 11,897 fish (1981) were enumerated. Fry size (g) in mid-summer was a significant correlate of mean smolt age and percent composition of age-2 smolts. We conclude that variation in smolt number and size, and thereby in adult returns, is mainly determined at the fry-to-1+ parr stage and thus the production of steelhead trout smolts is highly density dependent.

La dynamique de la population de truites arc-en-ciel (*Oncorhynchus mykiss*) dans un cours d'eau côtier de l'île de Vancouver (C.-B.) est à l'étude depuis 1976. Les estimations sur le nombre de géniteurs, la fécondité, le potentiel de ponte (n = 12 ans), l'abondance des alevins (n = 7 ans) et l'abondance des tacons (n = 2 ans) ont donné de l'information sur le taux de survie lorsqu'on les combine au dénombrement des smolts par année d'éclosion. La relation entre les oeufs et les alevins (un mois après l'émergence) était linéaire, à l'exception de 1976, année où les débits printaniers étaient exceptionnellement forts. Le taux moyen de survie de l'oeuf à l'alevin était de 6,5 % (min., 1,8 %; max., 11,5 %). Le taux moyen de survie de l'alevin au smolt était de 12,9 % (min., 3,3 %, max., 21,9 %). La relation entre les alevins et les smolts semblait indiquer un rendement asymptotique d'environ 7 500 smolts, soit 2,7 smolts pour 100 m^2 de rivière, selon le modèle du recrutement de Beverton-Holt. La production de smolts par année variait de 5 725 à 10 750. La variation était plus forte dans la production annuelle de smolts, qui se composait de quatre classes d'âge; on a dénombré de 2 104 (1978) à 11 897 poissons (1981). La taille des alevins (g) au milieu de l'été déterminait de façon significative l'âge moyen des smolts et la part en pourcentage de smolts d'âge 2. Nous concluons que la variation dans le nombre et la taille des smolts, et donc dans les remontes d'adultes, est déterminée principalement au stade alevin-tacon 1+, et donc que la production de smolts de truite arc-en-ciel dépend fortement de la densité.

Introduction

Wild steelhead trout are a highly-prized sports fish distributed throughout most streams of the western coast of North America. They are iteroparous and return as both summer-run and winter-run migrants which spawn in the spring. Fry emerge several weeks later, and rear through the parr stage in rivers before migration as smolts at ages of usually from 2 to 4 years (Withler 1966). Adult steelhead return after one to three years in the ocean and enter the sport fishery. To sustain this valued fishery under the pressures of commercial fishery interceptions (Hilborn and Walters 1977), habitat degradation (Larkin 1974; Hartman et al. 1983), and increasing angler effort (Billings 1988), steelhead management in British Columbia has necessarily become more intensive.

Until recently, steelhead management has not been complemented by intensive research on wild populations, and thus it has lacked supportive information on population dynamics. Most reported studies of steelhead trout have emphasized evaluations of hatchery fry and smolts (e.g., Wagner 1969; Slaney and Harrower 1981; Wentworth and LaBar 1984; Hume and Parkinson 1987; Seelbach 1987; Ward and Slaney 1990), or life history data obtained from anglers' catches (Maher and Larkin 1954; Narver 1969; Narver and Withler 1971; Hooton et al. 1987), or examined age and survival (smolt-to-adult) with a fish fence (Ward and Slaney 1988; Ward et al. 1989). Aside from an earlier study of a small stream in northern California (Shapovalov and Taft 1954) and comparisons of wild and hatchery migrants in Washington Rivers (Leider et al. 1986; Pevin and Hays 1989), little published information is available on the population dynamics of wild steelhead during the freshwater rearing stage.

We examined the survival from egg to smolt of seven broods of wild winter-run steelhead of the Keogh River on northern Vancouver Island (1976 to 1982). We estimated survivals from data including estimates of the adult population size, the size and fecundity of females, estimates of fry and parr abundance, and counts and ages of smolts migrating into the ocean. Here, we report on rates and variation in the egg-to-fry survival and fry-to-smolt survival, relating the latter to fry size and density.

Methods

The Keogh River is a coastal stream located in southwest British Columbia on northern Vancouver Island. It is 33 km in length and with a mean annual discharge of 5.62 $m^3 \cdot s^{-1}$, and is more fully described in Ward and Slaney (1979), Johnston et al. (1986), and Irvine and Ward (1989).

The procedure for deriving the population estimates and ages of adult steelhead and methods of enumerating and sampling smolts at the Keogh River are described elsewhere (Irvine and Ward 1989; Slaney et al. 1990; Ward and Slaney 1988, 1990; Ward et al. 1989; 1990). Briefly, smolts were enumerated through a counting fence near the mouth of the river during their downstream migration each spring; they were sub-sampled for age from scales from 1977 to 1979, then stratified random sampled for scales by 10-mm size intervals after 1980 (Ricker 1975; Ward and Slaney 1988). Adult numbers were based on Petersen mark–recapture estimates (Ricker 1975). Adult steelhead were marked (small hole on the edge of the operculum) as they migrated upstream, kelts were examined for marks when they left the river, and a Petersen population estimate was derived separately for each sex (Ward and Slaney 1988, 1990). Most of the females in the population were handled, either as upstream migrant adults, or unmarked kelts (mean, 77% from 1976 to 1982; Ward and Slaney 1988). The recapture rate of females marked in their upstream migration averaged 45%, and the rate of marking of the estimated number of females averaged 51% (Ward and Slaney 1988). Survival estimates from smolt to adult and variation in age structure of smolts and adults have been reported earlier (Ward 1988, 1989; Ward and Slaney 1988; Ward et al. 1989).

Total fecundity of an adult run of steelhead was determined from the population estimates of females and female lengths (Ward and Slaney 1988), and the log-linear relationship between female length and fecundity (n = 27; Bagenal 1967; Ricker 1968). Egg counts were performed on mature females which were sacrificed as they migrated through the fish fence near the mouth of the Keogh River. Atresia of eggs from the time of sampling to the time of spawning (1–3 months) was not likely a factor for this winter-run population, although this was untested. The fecundity of females sampled for length in each run was determined, and the geometric mean fecundity was calculated from length samples. Total fecundity for the run was the total fecundity of length-sampled females plus the average fecundity times the estimated number of unsampled females.

Potential egg deposition (PED) was calculated after subtracting mortalities or losses resulting from handling, sampling, broodstock collection for hatchery purposes (Slaney and Harrower 1981), and estimates of fish removed by anglers. Numbers of females removed by anglers were determined by requesting anglers to complete a questionnaire on cards at access points to the river from 1976 to 1980 (Ward and Wightman 1989). Agreement on number of fish killed with the annual steelhead harvest analysis (e.g., Anon. 1979) was within 5%. After 1980, fishery regulations were changed to catch-and-release. Estimates of PED were not corrected for egg retention because Shapovalov and Taft (1954) reported that steelhead were completely spent, having few, if any, eggs remaining in kelts. Thus, PED was equal to total fecundity less mortalities. For those years which included returns of hatchery adults (1981, 1982), PED was based on wild and hatchery females.

Steelhead fry and parr abundances were estimated for seven years and three years respectively, using similar techniques as those to determine Dolly Varden (*Salvelinus malma*) fry, as described in Smith and Slaney (1980). Briefly, densities were determined within habitat-stratified reaches of the Keogh River by electrofishing. Generally, a 3–4 step removal method was utilized (Seber and LeCren 1967) except within complex habitat where a Petersen mark-recapture method was employed (Ricker 1975). In 1978 and 1982, only the fry populations were sampled within 100-m sections in each reach, using the latter method. Total numbers were calculated based on average densities within five habitat strata, multiplied by the area for that strata, similar to the method of Hankin and Reeves (1988). Habitat strata and area were determined by visual classification and measurements, respectively, with the latter from calibrated range finders, over the entire river length (Ward and Slaney 1979). Fish ages were determined using length frequency to separate fry and parr, and ages of the latter were determined using the methods for smolts described in Ward and Slaney (1988). Differences in stream area were measured among years, and thus corrections to area-based population methods were based on the relationship between stream flow and width (e.g., Hogan and Church 1989). Although estimates of fry abundance were available for 1976 to 1982, sampling intensity in parr habitat was adequate only in 1976, 1977, and 1979. Owing to the more sporadic nature of parr distribution, greater area must be sampled to adequately estimate parr abundance (Hankin and Reeves 1988); thus, years where parr habitat was inadequately sampled were excluded from this analysis.

Fry weights were determined in late July to early August from 1976 to 1985 in representative reaches, and geometric mean fry weight for the main river was determined, as reported by Johnston et al. (1990). Mean weights used in this study were from km 28 to the river mouth, where the majority of fry rearing occurs, which excludes the short "control" section (3 km) reported in Johnston et al. (1990). However, since no data were available for the main river for 1981, their upstream "control" site was used to represent the river for that year. No whole-river fertilizer treatment occurred in 1981; mean fry size in their control section was not statistically different from the main river sites during untreated years (Johnston et al. 1990).

The relationships between annual mean fry weight and mean smolt age of a brood, and annual mean fry weight and the percent composition of age-2 smolts (arcsine-squareroot transformed) were determined by linear regression. Similarly, we regressed fry density on fry size (Sokal and Rohlf 1981).

The survival from egg to smolt was examined. Egg-to-fry survival was determined from PED and fry estimates. The relationship was examined by linear regression. Because egg-to-smolt and fry-to-smolt relationships were curvilinear, the Beverton-Holt curve was fitted in both relationships (Ricker 1975). The relationships between fry size and both fry density and fry-to-smolt survival rate were tested with linear regression techniques where survivals were transformed to the reciprocal of the natural logarithm of survival.

Results

The fecundity of adult females was positively and significantly related to fork length ($n = 27$):

$$\ln[\text{Eggs}] = 3.053\ln[\text{Length}_{\text{mm}}] - 11.89,\ r^2 = 0.51,\ p < 0.05$$

Using this relationship, measurements of female lengths from fish migrating upstream, and the population estimates of females, we determined the total fecundity of individual runs of steelhead from 1976 to 1982 (Table 1). PED (corrected for fish removals) was estimated to be highest in 1982, at ca. $2.6 \cdot 10^6$ eggs, and lowest in 1980, at only 466,000 eggs, representing a 5.6-fold difference in egg density. On average, ca. 6 eggs·m^{-2} (S.D. 3.4) were deposited annually in the main river (Table 1). Earlier investigations confirmed that few if any steelhead spawn in the main tributaries from which smolt production was insignificant (0-30 smolts·yr^{-1}·tributary^{-1}; data on file).

Population estimates of wild females and their fecundities suggested an average fecundity per female of 3,740 eggs during the study period. Hatchery females from net-pen reared smolts returned in 1981 and 1982, for an estimated 24,270 and 815,506 eggs from hatchery fish, respectively. The average length of wild adult females of the Keogh River (714 mm; Ward and Slaney 1988) suggested a slightly lower fecundity per female of 3,537 eggs, based on the length and fecundity relationship. Because wild adult numbers and ages varied biennially (Ward and Slaney 1988), annual PED also varied; even-numbered years (1976, 1978, 1980, 1982) averaged approx. 4,000 eggs per female whereas odd-numbered years (1977, 1979, 1981) averaged 3,300 eggs per female.

Fry density varied from 11 to 92 fish·100m^{-2} and averaged 34 fry·100m^{-2} over seven years (Table 1). When adjusted for small differences in stream width between years, estimates of total fry abundance averaged 85,860, with a high variation (SD, 77,821; Table 1). Mean fry weight was also variable annually, ranging from 0.4 to 2.03 g from 1976 to 1985 (Table 1).

Numbers of age-1+ and age-2+ parr were estimated during mid-summer for the three years 1976, 1977, and 1979. Respective age-1+ and age-2+ parr (±SE) were 6,063 (±1,929) and 3,969 (±2,036) in 1976, 10,869 (±1,585) and 5,433 (±1,233) in 1977, and 11,207 (±1,325) and 7,193 (±1,281) in 1979. Standard errors from habitat stratified sampling were larger for the estimates of age-2+ parr due to their lower abundance.

The number of smolts produced from each brood year varied from 6,071 to 10,750 fish (Table 1). Numbers of fish in each age-class were variable; e.g., composition of age-2 smolts averaged 33.2% and ranged between 12.1 to 82.3% (Table 1). Average yield from the river was ca. 2.6 smolts·100 m^{-2}, or, expressed as weight, 127 g·100 m^{-2}, for an average biomass yield of 336 kg (ca. 13.3 kg·ha^{-1}).

The relationship between PED and fry abundance was linear (Fig. 1), based on limited data ($n = 6$). Excluding the 1976 outlier, when flow during incubation and rearing was three times higher (5.1 m^3·s^{-1}) than the 10-yr average (1.6 m^3·s^{-1}), mid-summer fry abundance (F) and PED were positively correlated ($r = 0.97$) and described by:

$$\text{PED} = 0.102\text{F} - 23550.78,\ r^2 = 0.93,\ p < 0.05.$$

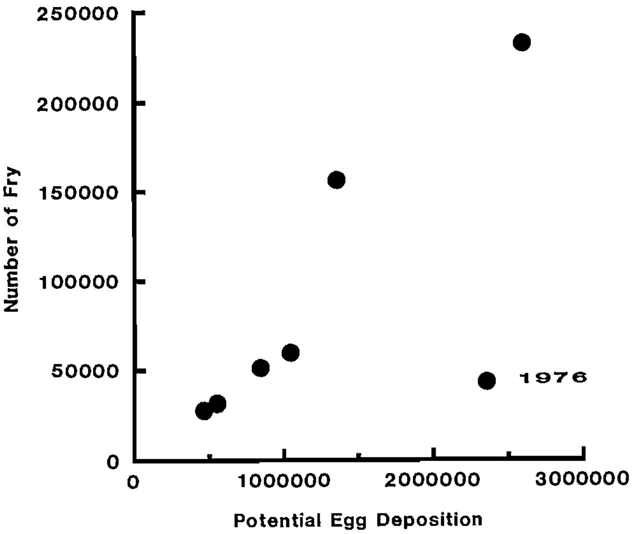

FIG. 1. The abundance of fry during mid-summer from 1976 to 1982 in relation to the potential egg deposition of adult steelhead of the Keogh River, B.C.

TABLE 1. Steelhead trout potential egg deposition, numbers of fry, fry weights, survival to the fry and smolt stage, and smolt yield by brood year in the Keogh River, 1976 to 1985.

Brood Year	Total Fecundity	Potential Egg Deposition	Fry/ 100 m² (1 SE)	Number of Fry (1 SE)	Mean Fry Weight (g)	Egg to Fry Survival (%)	Number of Smolts by Age				Total Smolts	Percent Age Composition					Egg to Smolt Survival (%)	Fry to Smolt Survival (%)
							age 2	age 3	age 4	age 5		age 1	age 2	age 3	age 4	age 5		
1976	2,529,039	2,356,227	17 (0.025)	42,840 (6,300)	0.40	1.82	1117	4892	561	118	6688	0	16.7	73.1	8.4	1.8	0.28	15.61
1977	1,110,000	1,043,623	24 (0.021)	59,724 (5,226)	0.70	5.72	835	3350	2713	16	6914	0	12.1	48.5	39.2	0.2	0.66	11.58
1978	1,424,000	1,355,242	62 (0.014)	156,240 (35,280)	0.75	11.53	1546	5592	104	0	7242	0	21.3	77.2	1.4	0	.53	4.64
1979	585,000	553,154	12 (0.020)	31,500 (5,250)	0.57	5.69	3474	2376	401		6251	0	55.6	38	6.4	0	1.13	19.84
1980	466,000	466,000	11 (0.007)	27,720 (1,764)	0.85	5.95	1504	3701	866		6071	0	24.8	61	14.3	0	1.30	21.90
1981	851,000	845,845	20 (0.045)	51,156 (11,510)	1.47	6.05	1951	3569	205		5725	0	34.1	62.3	3.6	0	0.68	11.19
1982	2,657,000	2,589,526	92 (0.206)	231,840 (51,912)	0.66	8.95	5291	2504	39		7834	0	67.5	32	0.5	0	0.30	3.38
1983					2.03		6600	1257	167		8024	0	82.3	15.7	2.1	0		
1984					1.65		8300	2443	7		10750	0	77.2	22.7	0.1	0		
1985					1.71		9786	287	108		10407	2.2	94	2.8	0	0		
Average	1,374,577	1,315,660	18	51,258	0.77	6.53	2245	3712	698	45	6675	0.0	33.2	56.0	10.5	0.3		
SD	891,900	847,068	28	67,860	0.34	3.03	1590	1178	933	64	727	0.0	20.9	17.1	13.5	0.7		

Thus, the ratio of eggs to fry was approx 10:1, except in the year of abnormal spring flow.

The egg-to-smolt relationship (Fig. 2) indicated density dependence (Ricker's α and β, 1.303×10^{-4}, and 18.64, respectively). Smolt yield reached an asymptote at ca. 7,500 fish, when egg deposition was 2.2×10^6 (Fig. 2), which corresponded to approx. 1,080 adults. Accordingly, only ca. 235 adults, or 4.4×10^5 eggs, would yield ca. 5,800 smolts, after which density-dependent mortality would reduce smolt output from the river. The fry-to-smolt relationship demonstrated density dependence (Fig. 3). Beverton-Holt parameters α and β were 1.284×10^{-4} and 1.137, respectively. Alternatively, the fry-to-smolt survival relationship may be based on fry density:

$$Y = 0.268 + 0.006D,\ r^2 = 0.995,\ p < 0.05.$$

where Y = the reciprocal of the natural logarithm of fry-to-smolt survival (%), and D = the number of fry per 100 m² of stream. Fry-to-smolt survival averaged 12.9% (min. 3.3%; max. 21.9% – Table 1). The above realation suggests that fry-to-smolt survival may achieve a maximum of ca. 40% at very low fry densities, and ca. 3.4% at carrying capacity, defined as the point where the replacement line meets the asymtote of the Beverton-Holt curve for fry and smolts.

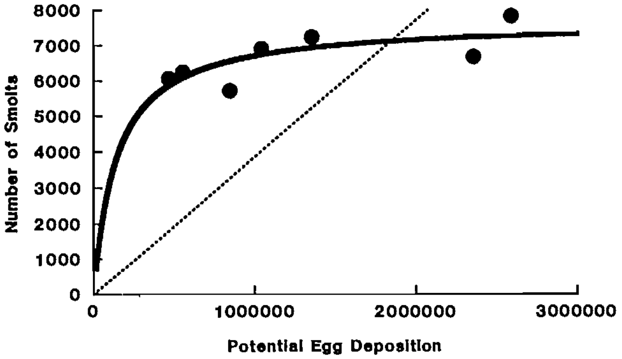

FIG. 2. Smolt yield within brood years and the potential egg deposition of steelhead of the Keogh River spawning in 1976 to 1982. The dashed line is the line of replacement assuming average smolt-to-adult survival and fecundity.

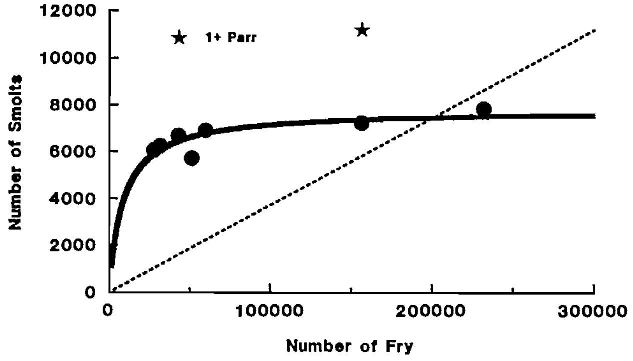

FIG. 3. Parr yield (star-shaped points, $n = 2$ yr) and smolt yield (circles, $n = 7$ yr) from fry abundance in the Keogh River, B.C. The continuous line is the Beverton-Holt curve fitted to the data. The dashed line is the line of replacement based on average smolt-to-adult survival, average fecundity, and egg-to-fry survival of 10%.

Fry-to-smolt survival at maximum sustainable yield was estimated as 13.4%.

Fry-to-parr (1+) survival was estimated at 25.4% and 7.2% for 1976 and 1978 fry, respectively. Fry-to-parr survival, although based on only two data points, appeared to be density-dependent (Fig. 3). Parr-to-smolt survival for 1+ parr only was estimated at 61.5% and 64.6% for 1976 and 1978 broods, respectively. Of the age 2+ fish from the 1977 brood which were sampled in 1979, 835 had already left as age-2 smolts (Table 1) and 7,193 were estimated to have remained in the river by that summer. Thus, the survival from 2+ parr to age-3 smolts and older was 84.5%.

Mean smolt age was positively correlated ($n = 10$, $r = 0.67$) with mean fry weight in mid-summer (Fig. 4b), but there was no relationship with fry density ($n = 7$, $r = 0.52$, $p > 0.05$). The relationship between mean smolt age and mid-summer fry weight expressed linearly was:

$$y = 3.112 - 0.484x,\ r^2 = 0.446,\ p < 0.05,$$

where y = mean age of smolts from a brood year, and x = the mean weight of steelhead fry in the brood year (mid-summer). Similarly:

$$y = 18.609 + 23.867x,\ r^2 = 0.501,\ p < 0.05,$$

where y is the arcsine-squareroot transformation of percent composition of age-2 smolts from a brood year (Fig. 4a). Fry density and fry size were not correlated ($r = 0.12$, $p > 0.05$).

Discussion

The egg-to-smolt and fry-to-smolt survivals of steelhead from the Keogh River were found to be dependent on fish density. Mid-summer fry abundance appears to be positively and linearly related to the number of eggs deposited by adult steelhead, as found by Bjornn (1987), but it was suggested that flow is a major factor. High flows have been suggested as a major cause of egg mortality in other salmonids (pink and chum, McNeil 1969; Atlantic salmon, Frenette et al. 1984; sockeye salmon, Thorne and Ames 1987). In the density-dependent relation between fry and smolts, fry size was a correlate of smolt age, whereas density was not, nor were density and size correlated. Because smolt age is related to smolt size, which ultimately affects adult returns from the sea (Ward and Slaney 1988; Ward et al. 1989), the importance of fry size cannot be underestimated. The egg-to-smolt and fry-to-smolt survivals determined in this study for steelhead trout at maximum smolt yield (or carrying capacity) and at maximum sustainable yield (Ricker 1975) are in close agreement with low and medium survivals, respectively, determined by Symons (1979) for Atlantic salmon of similar age (mean 2.8 yr; Ward and Slaney 1988).

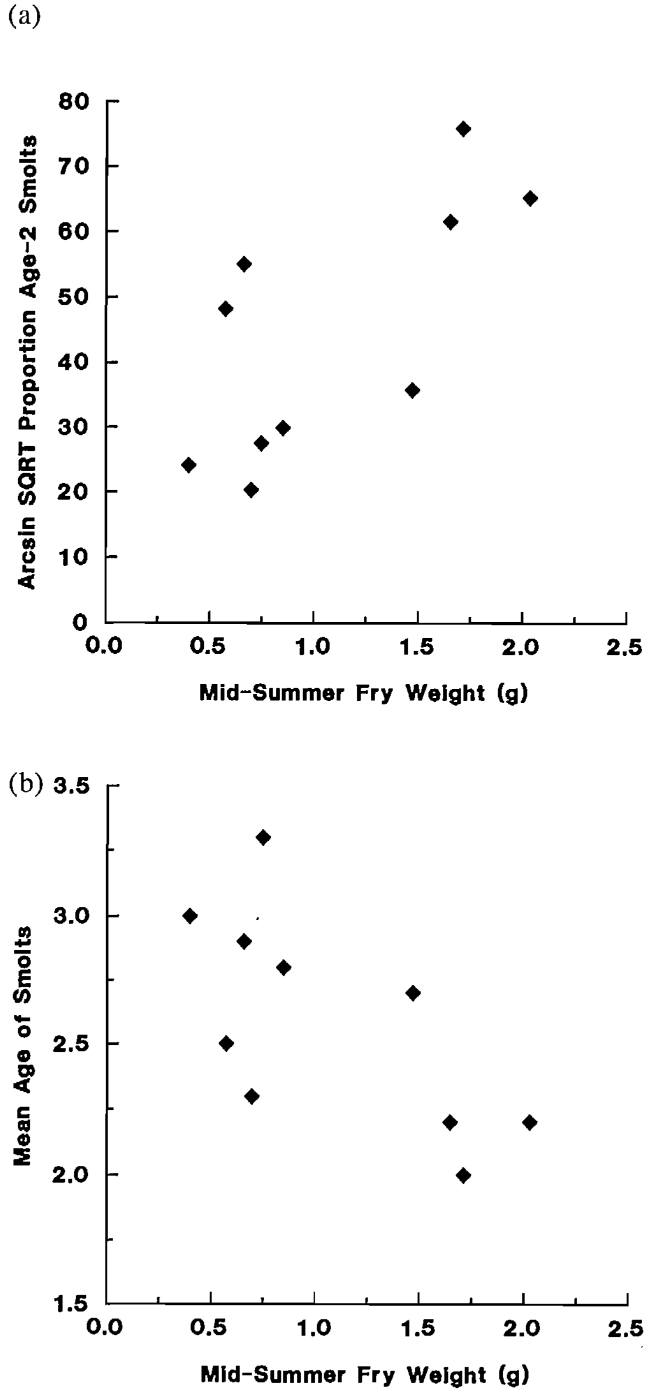

FIG. 4.(a) The proportion of age-2 steelhead smolts (arcsine squareroot transformation) in relation to the size fry attained by mid-summer in the Keogh River, and (b) mean age of steelhead smolts in relation to mid-summer fry weight in the Keogh River, from 1976 to 1985 broods.

Some of the variation in fry weight in this study was induced by whole-river fertilizer additions (Slaney et al. 1986; Johnston et al. 1990). The data suggested that age of smolts was correlated with mid-summer fry weight, the former expressed as either mean age or as composition of age 2-smolts. However, it is unclear what influence additional growth (induced by nutrient additions) at the age-1+ parr to the age-2 smolt stage may have had on the relationship between fry size and smolt age. Until this impact is clarified, caution must be utilized in interpretation of these results. Furthermore, the investigation of the relationship between fry size and density would have been confounded by the altered nutrient conditions of the river, but complete density data were not available during enriched conditions. Also, the relation of fry-to-smolt survival and steelhead fry size, as well as smolt age and fry size would likely have been different if based on late-summer fry size rather than mid-summer fry size. Scottish researchers have found that the smolt age of Atlantic salmon fry in the laboratory can be predicted from the size fry attained by late summer (Thorpe 1977; Metcalfe et al. 1988; Metcalfe 1991). Our results provide field evidence confirming their results, based on mid-summer fry size, but only three data points on late-summer fry sizes were available (Johnston et al. 1990), where fry size was large and smolts were predominantly age-2. Field studies are needed on the relationship of late-summer fry size and subsequent smolt yield.

In steelhead trout, density-dependent mortality occurs at the fry-to-parr stage based on both releases of hatchery fry (Bjornn 1978) and our results with wild fish, thus recruitment curves are asymptotic. Peven and Hays (1989) altered survival rates in a life history model of steelhead to determine which variables in the natural production equation would have the greatest effects on the population. Manipulation of survivals at the egg-to-smolt stage changed the estimates of adult abundance to the greatest degree. Our study agrees with that result, and further indicated that the most sensitive life stage controlling recruitment is from fry to parr.

A limited amount of data ($n = 7$) from the Keogh River demonstrated apparently asymptotic relations between eggs and smolts or fry and smolts. Additional data at high egg or fry densities probably would not significantly alter estimation of the asymptote, but more data at low densities, near the ascending portion of the Beverton-Holt curve, are required to more accurately define the parameters of Ricker (1975). Although our findings are preliminary in terms of actual curve shape until more years are examined, the results indicate that density dependence is an important factor controlling smolt production and adult returns of steelhead trout, and that variation in number likely occurs mainly at the fry to parr stage (i.e., ca. 30–110 mm). Ultimately, further research will lead to an optimum escapement model.

The density dependence detected in this study confirms similar results of fry releases and yearling migrant steelhead in the Lemhi River, Idaho (Bjornn 1978). Mortality rates were highest there in the first summer, but were independent of steelhead densities below 700 fry·100 m^{-2} which is much higher than densities in the Keogh River. However, there was only one data point in the density-dependent stage and several for the density-independent stage (Bjornn 1978). Density-independent mortality also plays a significant role, particularly in relation to storm events, as documented on stocked steelhead fry (Hume and Parkinson 1987) and wild sea trout fry (Elliott 1989). The relatively low survival from egg to fry in 1976 on the Keogh River was related to high flows.

Chadwick (1985) demonstrated that Atlantic salmon (*Salmo salar*) populations were below optimum escapement levels by examining the relationships between eggs deposited and smolts produced, or eggs deposited and adults produced in seven east coast Canadian streams where fish fences were operated. All relationships were linear, and further analysis in one of the streams (Western Arm Brook) confirmed that 8 out of 10 year classes showed near-constant survival in freshwater, with variations in year-class strength explained by egg deposition (Chadwick 1987). Chadwick and Randall (1986) demonstrated a linear relationship between Atlantic salmon kelts caught by anglers and 1+ parr captured in electrofishing surveys on the Miramichi River, New Brunswick. They argued that this suggests that the escapement was below optimum, since an asymptotic or domed-shaped relationship would have resulted otherwise. Also, Randall and Chadwick (1986) detected a positive correlation between age-0+ density and smolt production, again, based on intensive electrofishing over a 10-yr period. Such a linear relation would not be expected if density was sufficiently high to reduce production. The asymptotic levels of smolt yield by brood year in the Keogh River suggest escapement has been adequate under the current conditions of low harvest.

In contrast, Gee et al. (1978) developed dome-shaped recruitment curves between fry and pre-smolt Atlantic salmon parr, but at high fry densities (0.2–4.0 fry·m^{-2}). However, in a later study near Aberdeen, Scotland, Buck and Hay (1984) developed an asymptotic relationship between eggs deposited and numbers of migrant parr, where about 300,000 eggs (2.6 eggs·m^{-2}) were required to reach a level of 5,000 parr. Their results were based on capturing upstream migrant adults, habitat-stratified juvenile sampling and tagging, and downstream capture of juvenile migrants, during an 11-yr period.

From an extensive analysis of 18 years of data on a population of sea trout (*Salmo trutta*), Elliott (1989) showed that survival at different stages in the life cycle was strongly dependent on egg density. The relationship between eggs and emergent fry was found to approximate a Ricker curve (Ricker 1975) during the critical early stages of the life cycle. Evidence was strong for a critical period with high mortality in the first few weeks after fry emergence, after which density-dependent survival changed to proportionate survival, and the recruitment curve appeared nearly asymptotic (Elliott 1989). This work has led to a modified stock-recruitment model, with a time component that suggests maximum survivor density occurs at different egg densities as time progresses. Our fry samples were taken ca. 30 days after fry emergence; it's possible that a relationship between steelhead fry and smolts is a dome-shaped curve when based on newly-emerged fry.

Variation in age-specific survivals is important information for the management of fish populations (Clark et al. 1980; Taylor 1981). For example, increased food abundance and fry size (e.g., Johnston et al. 1990) may reduce early mortality at what Elliott (1989) refers to as the critical stage. Subsequent improvement to size-biased over-winter survival and increased growth could ultimately decrease residence time and lead to earlier age at smolting (Slaney et al. 1986). Similarly, increased cover could increase fry-to-smolt survival by adding space for rearing parr (Ward and Slaney 1979). Elucidation of the life stage experiencing the greatest mortality and the amount of variation in that mortality will provide further direction for management (Bjornn 1987). Based on a limited amount of data, our results indicate that mortality is highest for emergent fry as a function of density, as in Elliott (1989). During the first summer and through to the next spring, mortality continues to affect the majority of fish. Mortality rates decrease nearer to smoltification but more detailed research on age-specific mortality rates is required over the range in environmental conditions to describe the life history more fully.

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Determining the Relative Importance of Survival Rates at Different Life History Stages on the Time Required to Double Adult Salmon Populations

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FRYER, J. K., AND P. R. MUNDY. 1993. Determining the relative importance of survival rates at different life history stages on the time required to double adult salmon populations, p. 219–223. *In* R.J. Gibson and R.E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar,* in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

Two elementary population growth models (exponential and Beverton-Holt) are adapted to describe the success of efforts to double abundance of depressed anadromous salmonid stocks in the extensively impounded Columbia River Basin of the northwestern United States. To help policy makers understand the relative efficacy of improvements to hydroelectric passage and habitat, survivals were partitioned into the major life history stages that are most vulnerable to human interventions, the egg-to-smolt (or egg-to-dam) and the passage through a system of hydroelectric dams. In both models the number of years required to double the population proved to be highly sensitive to small changes in the egg-to-smolt survival rates when the population was increasing slowly. To achieve a population increase under Beverton-Holt at the nominal system average per-dam mortality rate of 11.5%, the smolt capacity had to be increased from 3 million to 12 million to enable doubling to occur at even the relatively high egg-to-smolt survival rates of almost 35%. In general, decreasing the per-dam mortality rate effected a far stronger reduction in doubling times than slight changes in egg-to-smolt survival rates.

Nous avons adapté deux modèles élémentaires de la croissance des populations (modèle exponentiel et modèle de Beverton-Holt) pour décrire le succès des efforts déployés pour doubler l'abondance des stocks affaiblis de salmonidés anadromes dans le bassin du fleuve Columbia (nord-ouest des États-Unis), qui compte un très grand nombre de retenues. Pour aider les autorités à comprendre l'efficacité relative des aménagements des passages dans les installations hydroélectriques et de l'habitat, nous avons réparti les taux de survie selon les grands stades biologiques qui sont les plus vulnérables aux interventions humaines, le stade de l'oeuf au smolt (ou de l'oeuf au barrage) et le passage dans une série de barrages hydroélectriques. Dans les deux modèles, le nombre d'années nécessaire pour doubler la population est apparu extrêmement sensible à des petits changements dans les taux de survie de l'oeuf au smolt quand la population était en augmentation lente. Pour obtenir une augmentation de la population selon le modèle de Beverton-Holt avec le taux moyen nominal de mortalité par barrage de 11,5 %, il fallait hausser la capacité de production de smolts de 3 à 12 millions pour qu'on observe un doublement, même avec des taux de survie relativement élevés de près de 35 % pour le stade de l'œuf au smolt. En général, la réduction du taux de mortalité par barrage amenait une baisse nettement plus forte du temps de doublement que de légères modifications dans les taux de survie de l'œuf au smolt.

Introduction

Under suitable environmental conditions, any given species is capable of increasing its population. Ecologists have become increasingly interested in measuring this rate of growth. In fisheries research, studies involving the rate of increase in populations have normally been associated with surplus production models (Graham 1935, Ricker 1958). The goal of these models has been to determine the number of surplus fish which can be harvested without reducing population sizes. Examination of such population models may determine the time required to allow depressed anadromous salmonid stocks to increase. This type of study is especially important in the Columbia River Basin where it is desired to double the number of adult salmon from its present level (Northwest Power Planning Council 1987). The importance of such studies is increased by the listing of Snake River chinook (*Oncorhynchus tshawytscha*) and sockeye (*O. nerka*) salmon under the federal Endangered Species Act (1973). To ensure the future of these stocks and their dependent fisheries, it is prudent to increase the populations as quickly as possible.

The success of efforts to restore depressed anadromous salmonid stocks in the extensively impounded Columbia River Basin of the northwestern United States is measured against the management goal of doubling the number of adult salmon from its present level. The doubling goal arose from the desire of policy makers for an easily understood means of measuring progress; yet, to our knowledge, the ability of an individual salmon recovery measure to contribute to the doubling goal has never been quantified. The models described in this paper offer a graphic means of understanding doubling time as a function of survival during a given portion of the life cycle.

Salmon recovery actions typically are intended to increase survivals at major life history stages that are most vulnerable to human interventions, such as the egg-to-smolt (or egg-to-dam) and the early portion of the smolt-to-adult (or dam-to-egg-deposition) stage during passage through the hydroelectric system. The need to divide the life cycle of the salmon into these segments for study was suggested by the information requirements of policy makers in order to address allocation of resources among various salmon recovery remedies. To help policy makers understand the relative efficacy of improvements at the two life history stages, the time required to double salmon populations was estimated using two population growth models, the exponential (Krebs 1978) and the Beverton-Holt (Beverton and Holt 1957). The Beverton-Holt approach also allowed an examination of the role of salmon production in determining the doubling time, where production is expressed as the numbers of smolts produced in a region.

The life history stages were selected to correspond to the types of salmon recovery remedies available. During the earliest life history stage, egg-to-smolt (egg-to-dam, from egg deposition to the first encounter with a dam on the Columbia or Snake rivers), non-natural mortalities are associated with deleterious habitat alterations, such as compaction or burial of spawning beds, increases in water temperatures, increased predation, and increased juvenile migrant mortality. Remedies to problems during the first life history stage involve alterations in land use practices of the timber harvesters, the irrigators, and land use managers. During the second life history stage, smolt-to-adult (dam-to-egg-deposition, from first encounter with a major dam to spawning), non-natural mortalities are associated with dam and reservoir passage conditions and fishing. The dam passage mortality was selected for study because it accounts for the majority of human-induced mortality during this life history stage. Dam-passage mortality is of particular interest to policy makers because its remedies are expensive and take long periods of time to implement. Even though a seemingly insignificant decrease in the passage mortality rate from the present estimate of 11.5% to 10% at each dam would be financially and politically costly to implement, it could be readily justified if it is necessary for the salmon populations to persist or if salmonid populations could be shown to double in a much shorter period of time.

Life history values from the Snake River spring chinook salmon populations are used in the examples because the existence of this stock is particularly precarious. The juveniles and adults must survive passage of eight mainstem dams between their spawning grounds and the sea, and the habitat upland of the spawning grounds is heavily used for agricultural pursuits, including timber harvest. The Snake River spring chinook formally became a threatened species on May 22, 1992.

Methods

Exponential and Beverton-Holt (1957) population growth models were used to estimate the number of years required to double population size for different smolt-to-adult survival obtained by varying hydroelectric passage survival rates for juveniles as well as for different egg-to-smolt (egg-to-dam) survival. Values of variables were taken from other current models of Snake River spring chinook salmon populations (Northwest Power Planning Council 1989; Earl Weber, Columbia River Inter-Tribal Fish Commission, personal communication): 50% of returns were females, 4200 eggs per female, a 5-year life cycle, and initial smolt-to-adult survival rate of 0.004. In the exponential model, the egg-to-smolt survival rate was varied from 0.10 to 0.40. For the Beverton-Holt model, the egg-to-smolt survival rate was also varied from 0.10 to 0.40 and the initial smolt capacity was set at 3,300,000 fish.

Exponential Model

In the exponential population model (Krebs 1978),

$$(1)\quad N_t = N_0 \exp(-z)$$

where N_t is the population size after 5 years, N_0 is the initial population size and z is the instantaneous rate of mortality (the sum of instantaneous rates of mortality from egg to smolt and from smolt to adult). The present value for N_t is substituted recursively into the equation as the next value of N_0 to obtain a new value for N_t. If N_t is greater than N_0, the process continues until the population doubles. If N_t is less than or equal to N_0, the population will not double.

To examine the role of dam-passage mortality in the time required to double the population, equation (1) was modified to

$$(2)\quad N_t = N_0 P \exp(-z)$$

where P is the survival rate during outmigration and z now represents the total instantaneous mortality rate, excluding passage mortality. Therefore, z represents the sum of the instantaneous egg-to-start-of-outmigration and saltwater-entry-to-adult mortality rates.

Beverton-Holt Model

In the Beverton-Holt population model, the actual egg-to-smolt survival rate depends upon the smolt capacity, and is calculated as (Beverton and Holt 1957)

$$(3)\quad S_a = S_e\,[1+(N_0 F E S_e)/K)]^{-1}$$

where S_a is the actual egg-to-smolt survival rate, S_e

is the estimated egg-to-smolt survival rate, N_0 is the initial population size, F is the percentage of females, E is the number of eggs per female, and K is the smolt capacity. The population size after one life cycle is defined as

$$(4)\quad N_t = N_0 S_a \exp(-z_1)$$

were z_1 is the instantaneous smolt-to-adult mortality rate. Initially, N_0 was set as

$$(5)\quad N_0 = \frac{QK}{S_a FE}$$

where Q is the number of smolts, expressed as a proportion of the smolt carrying capacity. Values of Q (the seeding rate) varied from 0.10 to 0.50.

To examine the role of passage mortality in the time required to double population sizes, equation (4) was modified as

$$(6)\quad N_t = N_0 S_a P \exp(-z_1)$$

where P is the survival rate during outmigration, z_l represents the saltwater-entry-to-adult mortality rate, and S_a is the actual egg-to-start-of-outmigration survival rate.

Example

As of 1991, the number of naturally spawning Snake River spring chinook had declined to approximately 3,000 fish (Columbia River Inter-Tribal Fish Commission 1991). Downstream migration past eight dams causes high mortality to smolts. The mortality rate at each dam-and-reservoir combination (hereafter referred to as the per-dam mortality rate) is estimated to be 11.5%, resulting in a cumulative downstream migration survival rate of 37.8% for a route encompassing eight dams. (All data for this example were obtained from the Northwest Power Planning Council's system planning model [Northwest Power Planning Council 1989]). The estimated saltwater-entry-to-adult survival rate is 0.54%. The estimated spring chinook smolt capacity of the Snake River is 3,300,000 fish (Earl Weber, Columbia River Inter-Tribal Fish Commission, personal communication). The estimated egg-to-smolt survival rate is 26% but this parameter was allowed to vary from 10 to 40% to simulate different levels of habitat quality. The two models were run for differing per-dam mortality rates. For the Beverton-Holt model, the smolt capacity was increased when populations failed to double using reasonable values for other parameters.

Results

The number of years required to double the population proved to be highly sensitive to small changes in the egg-to-smolt survival rates at rates where the population was increasing slowly (Fig. 1). For the exponential model, increasing the egg-to-smolt survival rate from 12.6 to 14.2% decreased the time required to double the population from 65 years to 20 years. However, at higher survival rates ranging from 17.0 to 23.8%, the time required to double the population remained constant. Doubling time for the Beverton-Holt models was also highly sensitive to small changes in the egg-to-smolt survival rate when the population was increasing slowly.

The time required by the exponential model to double the Snake River spring chinook salmon population was highly dependent upon both per-dam mortality and egg-to-smolt survival rates (Fig. 2). At an egg-to-smolt survival rate of 27%, a drop in the mortality rate from 11.5 to 10.0% decreased the number of years required for doubling from 55 years to 20 years.

To double the population in a twenty-year period, the two models required different egg-to-smolt survival rates (Fig. 1). With the exponential growth model, population sizes doubled in 20 years at an egg-to-smolt survival rate of 14.2% compared to 16.4% for the Beverton-Holt model initially seeded at 10% of smolt capacity. As the initial smolt population was increased for the Beverton-Holt model, the time required for

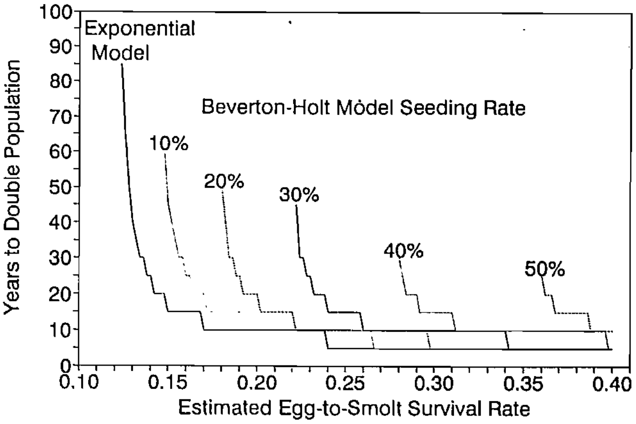

FIG. 1. Years required to double salmonid populations for a Beverton-Holt population model with initial seeding rates of 10, 20, 30, 40, and 50% and an exponential population model.

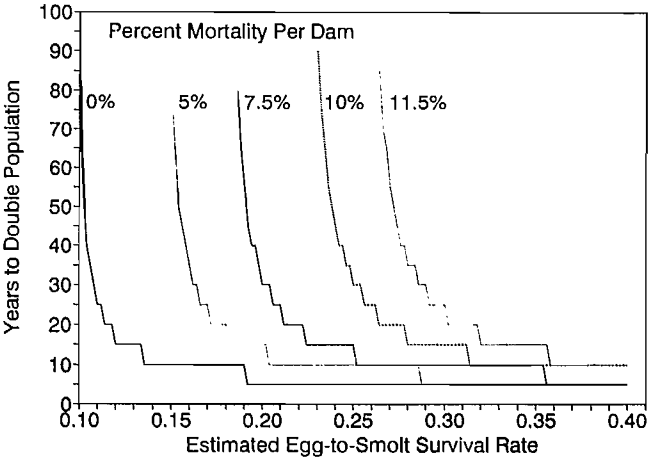

FIG. 2. Years required to double Snake River spring chinook salmon populations as a function of egg-to-smolt survival and per-dam mortality rates for the exponential population model.

doubling also increased and higher egg-to-smolt survival rates were necessary.

The Beverton-Holt model results emphasized the importance of the per-dam mortality rate on the time required to double the Snake River spring chinook salmon population (Fig. 3). With the smolt capacity limited to 3,300,000 and a per-dam mortality rate of greater than 6%, populations did not double unless the estimated egg-to-smolt survival rate is increased to almost 40%. Relatively small percentage decreases in per-dam mortality rates could be substituted for much larger percentage increases in egg-to-smolt survival rates.

To achieve a population increase at an 11.5% per-dam mortality rate, the smolt capacity was increased to 12,000,000. Doubling then occurred at estimated egg-to-smolt survival rates of almost 35% (Fig. 4). Decreasing the per-dam mortality rate had a far more beneficial effect than slight changes in egg-to-smolt survival rates.

Discussion

While such simple models cannot capture the complexity of real life, their very simplicity allows policy makers to develop an awareness of the importance of making coordinated investments in increasing hydroelectric passage survivals, the numbers of salmon produced, and improving habitat quality. While improving per-dam survivals is clearly crucial to successful doubling, such success is unlikely for Snake River spring chinook salmon without more than four-fold increases in the numbers of juvenile salmon produced. Even with four-fold increases in the number of juveniles produced, however, extremely high egg-to-smolt (egg-to-dam) survival rates are necessary to double population size given present smolt-to-adult survival rates. Decreasing mortality rates at the dams, the most likely means of increasing the smolt-to-adult survival rate, had a far greater impact on the rate of increase in the modeled population than any other modeled remedy. This was particularly evident for the Beverton-Holt model; it was difficult to increase the number of smolts because the density-dependent nature of this model would result in a corresponding decrease in the egg-to-smolt survival rate. Therefore, the key to increasing the population size in such a model is to increase the smolt-to-adult (dam-to-egg-deposition) survival rate.

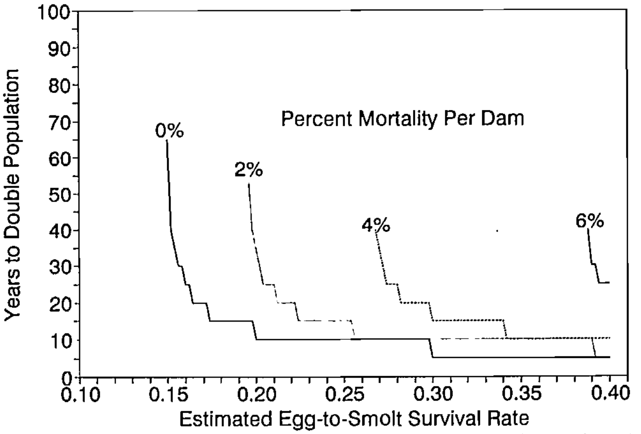

FIG. 3. Years required to double Snake River spring chinook salmon populations as a function of egg-to-smolt survival and per-dam mortality rates with a smolt production capacity of 3,300,000 for the Beverton-Holt population model.

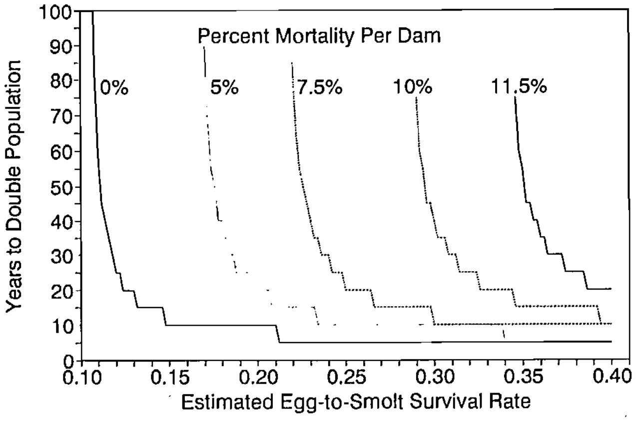

FIG. 4. Years required to double Snake River spring chinook salmon populations as a function of egg-to-smolt survival and per-dam mortality rates as a smolt production capacity of 12,000,000 for the Beverton-Holt populatuion model.

Conclusions based on the models hold out some hope that simultaneous improvements in freshwater habitat quality, juvenile salmon production, and downstream passage survival could permit the region to achieve its salmon recovery goals during the next twenty years. On the other hand, implementing remedies individually would appear to require draconian changes in the operation of some major industries, such as the hydroelectric power system, the irrigated agriculture, or the timber industry. Furthermore, the model results point out that even radical alteration in any single major source of mortality is unlikely to achieve the salmon recovery goal of the region. Thus the wisdom of the politically motivated approach of sharing the burden of salmon recovery across all sectors of the regional economy is supported by the technical arguments of the models.

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Compensatory Growth and Optimum Size in One-Year-Old Smolts of Atlantic Salmon (*Salmo salar*)

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The relationship between freshwater growth during the spring prior to seaward migration and final size of river age 1 Atlantic salmon (*Salmo salar*) smolts was examined in three rivers of northern Spain using back-calculation procedures. For each river and smolt year considered separately, growth during the first year was positively correlated with smolt size, but negatively correlated with the subsequent spring growth. At the first winter, 1^+ smolts (with spring growth) were smaller than 1° smolts (without spring growth), but they attained the same size at smolting. Smolt size differed significantly between years and more clearly between rivers. Interannual variation in mean smolt size was synchronized in two rivers, suggesting some common climatic influence. There was an inverse relationship between autumn water discharge (October–December) and growth during the first year in the three rivers. Spring growth was positively correlated to discharge in one river and to air temperatures in another one. Our results suggest that environmental factors influence size at smolting, but deviations from an optimal length range are diminished by an effect of growth compensation.

La relation entre la croissance en eau douce pendant le printemps qui précède l'avalaison et la taille finale des smolts de saumon atlantique (*Salmo salar*) d'âge 1 en rivière a été examinée dans trois cours d'eau du nord de l'Espagne par des méthodes de rétrocalcul. Chaque cours d'eau et chaque année de croissance étant considérés séparément, la croissance pendant la première année était positivement corrélée à la taille des smolts, mais négativement corrélée à la croissance du printemps suivant. Au premier hiver, les smolts 1+ (après croissance printanière) étaient plus petits que les smolts 1° (sans croissance printanière), mais ils atteignaient la même taille à la smoltification. La taille des smolts différait de façon significative d'une année à l'autre, et plus nettement d'un cours d'eau à l'autre. La variation interannuelle dans la taille moyenne des smolts était synchronisée dans deux cours d'eau, ce qui peut révéler une certaine influence similaire du climat. Il y avait une relation inverse entre le débit de l'eau à l'automne (octobre–décembre) et la croissance pendant la première année dans les trois cours d'eau. La croissance printanière était positivement corrélée au débit dans un cours d'eau et à la température de l'air dans un autre. Nos résultats semblent indiquer que les facteurs environnementaux influent sur la taille à la smoltification, mais que les déviations par rapport à une fourchette optimale de longueur sont minimisées par un effet de croissance compensatoire.

Introduction

The transition between the freshwater and marine environments is one of the critical periods in the life-cycles of anadromous salmonids. Time of seaward migration and smolt size are likely the most important factors influencing early marine survival (Bilton et al. 1982; West and Larkin 1987; Lundqvist et al. 1988; Skilbrei 1989; Ward et al. 1989; Mathews and Ishida 1989; Henderson and Cass 1991; but see Holtby et al. 1990). In Atlantic salmon (*Salmo salar*) populations, anadromous individuals leave their natal streams after a period that varies widely throughout their geographical range, and is dependent upon the growth conditions prevailing in those rivers (Metcalfe and Thorpe 1990). Among the physical factors influencing freshwater growth, temperature is perhaps the most evident (Johnston and Saunders 1981; Morrison 1989; Thorpe et al. 1989; Berg et al. 1990; Metcalfe and Thorpe 1990; Jensen 1990). To a lesser extent, growth and survival have been related to river discharge (Slaney and Northcote 1974) and, in addition, water temperatures and river discharge have been identified as important factors in regulating the time of downstream migration (Gibson and Côté 1982; Hesthagen and Garnås 1986). On the other hand, the duration of the freshwater phase appears to be related to the physiological and ecological advantage of attaining a minimum size to enter the marine environment (Johnston and Saunders 1981; Bilton et al. 1982; Lundqvist et al. 1988). Hence the size at smolting might be adjusted by selection to local environmental conditions, as suggested by the relative intra-population stability of this trait (Hesthagen and Garnås 1984; Gibson and Côté 1982).

Seawater acclimation is subjected to an endogenous circannual rhythm in which the hypoosmoregulatory ability of smolts peaks during a narrow period (Eriksson and Lundqvist 1982; Lundqvist and Eriksson 1985; McCormick et al. 1985; Hansen and Jonsson 1989). Out of this 'smolt-window', downstream movements seem to be not true seaward migrations, since the physiological transformations involved in the smoltification process are not completely developed

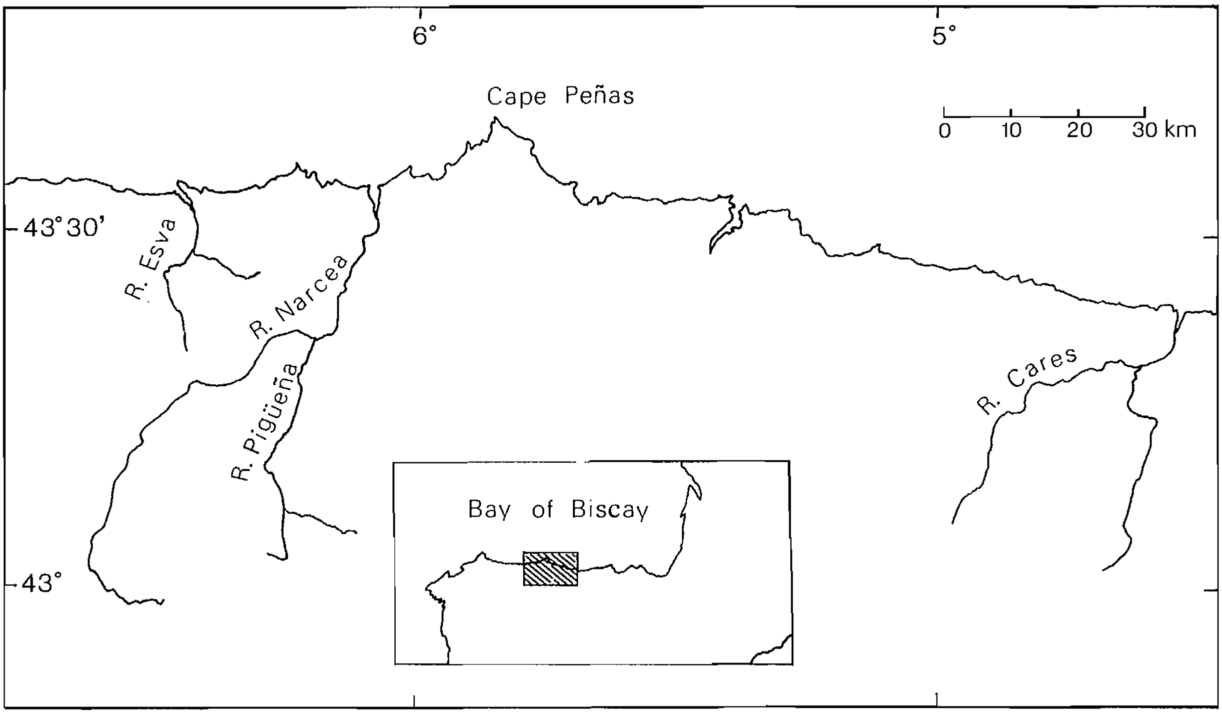

FIG. 1. The north coast of Spain and location of the study rivers.

(Virtanen 1988; but see Cunjak et al. 1989). Thus, the opportunity to initiate the marine growth would rise at discrete time intervals.

The purpose of this study was to determine whether smolt size is fixed within populations. In river age 1 salmon, growth to the smolt stage occurs in two intervals: growth up to annulus formation or first-year growth, and growth from annulus formation to smolting or spring growth. If smolt size is fixed, then small age 0+ parr should have greater spring growth than large age 0+ parr. We test this hypothesis by back-calculating growth from adult scales over a 9 year period in three rivers. In addition, we test for effects of environmental variables thought to be predictive of growth opportunity or timming of seaward migration on each growth component.

Methods

Study rivers are located in northern Spain (Fig. 1). The Narcea River has a catchment area of 1849 km^2. The mean flow during 1985–89 was 56.0 m^{3}s^{-1}. The Esva River has a catchment area of 467 km^2 in a region characterized by siliceous bedrock, and the mean flow during 1985–89 was 9.9 m^{3}s^{-1}. The Cares River is a 4th order stream with a catchment area of 1120 km^2 and runs on calcareous bedrock; the mean flow was 17.8 m^{3}s^{-1}.

The Atlantic salmon stocks of these rivers mainly consist of two-sea-winter salmon (50–90 %), but there are appreciable proportions of grilse and multi-sea-winter salmon; they are Type III stocks according to the terminology used by Porter et al. (1986). On average, annual angling catches were (x ± SD) 714 ± 426, 325 ± 200, and 544 ± 233 fish for the Narcea, Esva, and Cares rivers, respectively. Detailed information on total numbers and sea age composition of angling catches between 1974 and 1989 has been reported by Nicieza et al. (1990). Smolt migration occurs from February to May, and it appears to peak during March–April (Nicieza et al. 1991).

Scale samples, length, weight and date of capture from most of the fish caught by angling during the period 1985–91 were taken by the staff of the Agencia del Medio Ambiente del Principado de Asturias. Scales from fish captured in 1986 were not available for study. Scales collected on the Cares River during 1987, and on the Narcea River during the second half of the angling season of 1989 were also lost. To avoid confusing effects derived from differences in growth rates, the main analyses were restricted to river age 1 fish. Age 2 smolts were not abundant enough through all the rivers and years, and therefore it was not possible to perform a separate analysis. For back-calculation procedures, random samples of 50 or more fish were taken for each combination of river, catch year and age-class (1.1, 1.2, 1.3) if available (sample sizes in Table 1). We also selected some samples of river age 2 salmon for back-calculation procedures. For each fish, from two to six scales selected among the largest, most normally shaped, and having no regenerate nucleus were cleaned and mounted between two glass microscope slides. Scale radii corresponding to the end of the first growth period, smolt phase, and total radius were measured (± 0.01 mm) using an image analyzer (IMCO-10 system and MIP software). To discriminate between freshwater and saltwater zones on the scale, we used the criteria described by Mathews and Ishida (1989): thickness, spacing, and curvature of the circuli. In juvenile fish, circuli on the scale's posterior portion were always closed inward; the point in which circuli were opened outwards was then considered as the limit of the freshwater phase. In addition, we used simultaneous examinations of juvenile scales and adult scales to identify the demarcation between the freshwater and marine zones. All scale samples, including that not used for back-calculation analysis, were read for age determination.

The relationship between scale radius (R) and fork length (L) was examined in the rivers Esva and Narcea, for which samples of juvenile and anadromous salmon were available. For the Narcea River, scales of 253 juvenile (ages 0+ to 2+) and 943 anadromous salmon (age classes 1.1, 1.2, 1.3, 2.1, 2.2, 2.3) were included in the analyses. The data set of the Esva River was composed of 97 juvenile and 530 adult salmon. Four functional age-groups were considered: juvenile and 1-, 2-, and 3-sea-winter salmon. After examination of the studentized residuals, the ten worst outliers of each subset, including all cases with absolute values greater than 3.00, were eliminated from the L–R regressions. Analysis of covariance was performed to determine which regression model provided the best fit to the data (Bartlett et al. 1984). The best results (fit of the overall data sets, fit of the mean values of each age-class, and homogeneity of slopes for the lines through separate age-groups) were obtained after $\log_{10}$-transformation of L and R. In the second step of the back-calculation procedure, body lengths were calculated from annular scale radii by using formulae applicable to the scale proportional (SPH) and body proportional (BPH) hypotheses (Francis 1990), and the parameters estimated in the first step. To have an additional source of comparation, we also attempted the widely used Fraser–Lee method. As measure of the disagreement between back-calculation methods, we used the mean of the maximum relative deviations (d) between the estimates from two different back-calculation methods:

$$d_{it} = (e_a - e_b) / \min(e_a, e_b)$$

where d_{it} is the deviation for case i at time t, and e_a, e_b are the lengths estimated from two different back-calculation methods.

Daily discharge in the rivers Narcea, Esva and Cares were supplied by the Confederación Hidrográfica del Norte de España. Eight variables (D1 to D8) were derived from sums of monthly means (Table 6). Since water temperature data were not available, air temperatures (available from the Instituto Nacional de Meteorología) were used to obtain T1 to T9 (Table 6). For a non-continuous record from the Pigüeña river (Narcea basin), air temperatures were highly correlated with water temperatures ($r = 0.918$, $P < 0.001$, $n = 32$)

One-way analysis of variance was utilized to test for differences in growth during the first year (RW1) and smolt size (S) between 1.1, 1.2, and 1.3 salmon from the same smolt year. Sample variances were not homogeneous in two comparisons (Bartlett–Box test), so we also used the non-parametric Mann-Whitney U-test on these data. Regression and correlation analyses were performed to describe the relationships between RW1 and spring growth (SG) and to test for effects of discharge and temperature on RW1 and SG. River and year effects on smolt size were tested by using two-way ANOVA restricted to the 1.2 age-class, for which random samples of 50 individuals could be taken. Statistical analyses were done with the SPSS/PC+ and SAS computer packages; all quoted probabilities are for two-tailed tests, and the rejection level was set at $\alpha = 0.05$.

Results

Relationships between Body Length and Scale Radius

For both Narcea and Esva rivers the line fitted through the mean values of L and R for each age group (Fig. 2; juvenile, and sea ages .1, .2, and .3) did not

TABLE 1. Number of river age 1 salmon for which back-calculation was performed by catch years and age-classes, and mean number (x) of scales measured by fish.

	Narcea				Esva				Cares			
catch year	1.1	1.2	1.3	x	1.1	1.2	1.3	x	1.1	1.2	1.3	x
1985	8[a]	28	54	2,68	—	—	—	—	—	—	—	—
1987	126	134	17[a]	1,98	28[a]	53	2[a]	2,76	—	—	—	—
1988	76	85	7[a]	2,96	25[a]	60	3[a]	2,75	50	51	2[a]	2,62
1989	6[b]	51	17[a]	2,95	26[a]	51	—	1,80	44[a]	51	3[a]	2,22
1990	58	75	1[a]	2,92	29[a]	51	—	2,89	37[a]	50	1[a]	2,79
1991	51	68	2[a]	2,84	24[a]	52	—	3,17	48[a]	52	1[a]	2,93

[a] No more fish were caught or scale sampled.

[b] 1989 scale sample was partially lost.

differ from a straight line (ANCOVA: Narcea, $F_{2,1178} = 0.807$, $P > 0.5$; Esva, $F_{2,609} < 0.001$, $P > 0.9$). Slopes of the overall regression lines were not significantly different between rivers (ANCOVA, $F_{1,1799} = 2.80$, $P > 0.09$; Fig. 3) and there were no differences among adjusted means ($F_{1,1800} = 0.449$, $P > 0.5$). Therefore, a unique data set (Narcea-Esva) and linear regressions were used to determine the parameters associated to SPH and BPH back-calculation hypotheses, obtaining the following regression lines

$$\log L = 1.141 + 1.052 \log R$$
$$\log R = -1.056 + 0.934 \log L$$

and the back-calculation formulae:

$$L_i = 10^{1.131 + (\log Ri / \log R)(-1.131 + \log L)} \quad \text{(SPH)}$$
$$L_i = 10^{[(1.141 + 1.052 \log Ri) / (1.141 + 1.052 \log R)] \log L} \quad \text{(BPH)}$$
$$L_i = 10^{[(\log Ri / \log R)(\log L - 1.141)] + 1.141} \quad \text{(Fraser-Lee)}$$

where L and R are the body length (cm) and scale radius (mm) at time of capture, Li and Ri are the corresponding values at the time of formation of ith scale mark. Back-calculations of lengths of adults from Narcea, Esva, and Cares rivers were made using these three expressions.

BPH and Fraser-Lee equations provided similar results, although BPH lengths were slightly greater: the mean differences in RW1 ranged from 0.04 cm for the Esva River to 0.17 cm for the Cares River. Absolute differences in smolt size averaged from 0.06 cm (Esva) to 0.19 cm (Cares). For both RW1 and S, lengths obtained from SPH method were about 0.3–0.5 cm less than by BPH or Fraser-Lee formulae. The mean relative deviation with respect to the minimum estimate obtained from any back-calculation method, was in all cases less than 6% (ranges: 2.40–5.97% and 1.99–4.80% for RW1 and S respectively), and similar in all three rivers, suggesting that back-calculation imprecision was low. Since both BPH and SPH methods seem equally acceptable (Francis 1990), we used SPH back-calculated lengths in the following analyses as this method provided more conservative results. RW1, SG, and S back-calculated in this manner were consistent in ranges and mean values with actual lengths of juvenile salmon in the Pigüeña and Esva rivers (Nicieza et al. 1991).

Winter Size / Smolt Size Relationships

There were no significant differences in RW1 or S among sea ages in most years. However, in the Esva and Cares rivers, mean values of both RW1 and S were greater for the 1.1 age-class than for the 1.2 age-class over all years (Tables 2 and 3). In the Narcea River, RW1 and S were larger for 1.2 salmon than for 1.1 salmon in two of four years (Table 4).

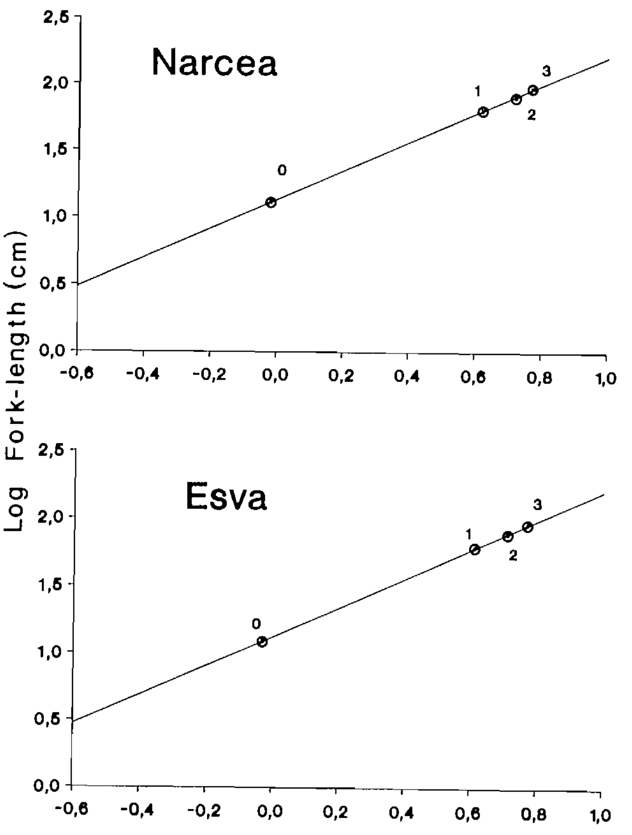

FIG. 2. $\log_{10}$–$\log_{10}$ plot of mean fork length vs. mean scale radius for the age-groups (0, 0+ and 1+ juvenile; 1, 1.1; 2, 1.2; 3, 1.3) considered in the rivers Narcea and Esva.

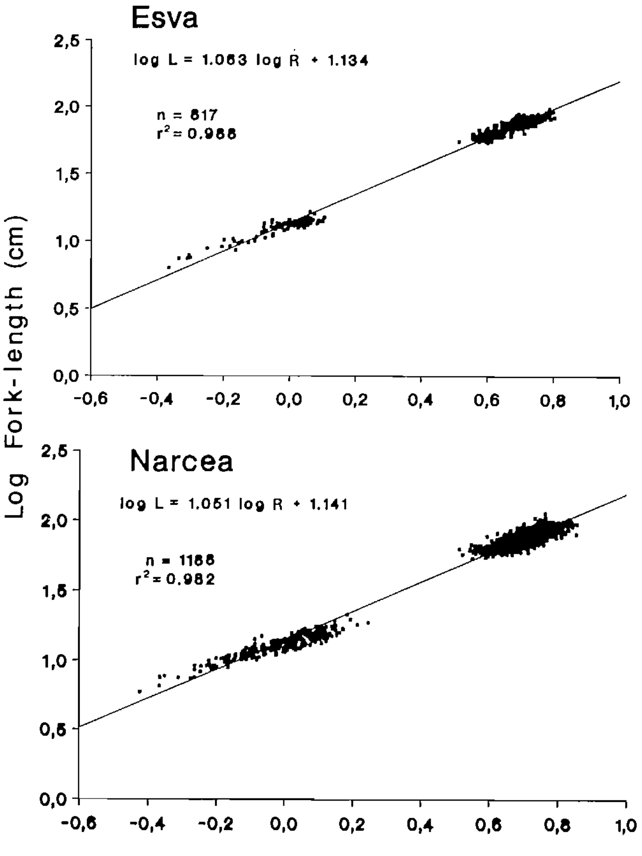

FIG. 3. Scattergram of fork length and total scale radius ($\log_{10}$–transformed) for juvenile and anadromous salmon from rivers Narcea and Esva, and least squares regression lines.

TABLE 2. Mean values (*X*) and standard deviation (SD) of back-calculated lengths (cm) at the first winter (RW1) and at smolting (S), and sample sizes (N) for adult salmon of the river Esva. Significance of *F*-tests: * $P < 0.05$; NS, nonsignificant.

	RW1				S				N		
Smolt year	1.1 *X* SD	1.2 *X* SD	1.3 *X* SD	*P*	1.1 *X* SD	1.2 *X* SD	1.3 *X* SD	*P*	(1.1)	(1.2)	(1.3)
1984	—	—	11.0	—	—	—	14.9 —	—			(2)
1985	—	11.1 (1.9)	13.0 (2.0)	—	—	14.7 (1.3)	14.9 (2.7)			(53)	(3)
1986	13.0 (2.3)	12.2 (2.3)	—	ns	15.9 (1.9)	15.1 (1.6)	—	ns[a]	(28)	(60)	
1987	11.6 (1.9)	10.9 (2.2)	—	ns	15.0 (1.6)	14.8 (1.5)	—	ns	(25)	(51)	
1988	11.1 (1.5)	10.7 (2.0)	—	ns	15.7 (1.5)	14.8 (1.9)	—	ns[a]	(26)	(51)	
1989	12.8 (2.2)	11.5 (2.2)	—	*	15.3 (1.9)	14.6 (1.5)	—	ns[a]	(29)	(52)	
1990	13.0 (2.6)	—	—	—	16.6 (1.9)	—	—	—	(24)		

[a] $0.05 < P < 0.06$.

TABLE 3. Mean values (*X*) and standard deviation (SD) of back-calculated lengths at the first winter (RW1, cm) and at smolting (S), and sample sizes (N) for adult salmon of the river Cares. Significance of F-tests: ** $P < 0.01$; NS, nonsignificant. If not indicated, assumption of homogeneity of variances was satisfied (Bartlett–Box *F*-test, $P > 0.05$).

	RW1				S				N		
Smolt year	1.1 *X* SD	1.2 *X* SD	1.3 *X* SD	*P*	1.1 *X* SD	1.2 *X* SD	1.3 *X* SD	*P*	(1.1)	(1.2)	(1.3)
1985	—	—	10.1	—	—	—	16.0 —	—			(2)
1986	—	12.9 (2.5)	15.6 (0.4)	—	—	16.3 (2.3)	19.4 (1.5)	—		(51)	(3)
1987	13.6 (3.1)	12.9 (2.4)	13.2	ns	17.3 (2.9)	16.4 (2.4)	16.2	ns	(50)	(51)	(1)
1988	13.6 (2.8)	11.9 (2.2)	13.6	**	17.3 (2.3)	15.9 (2.3)	16.6	**	(44)	(50)	(1)
1989	14.3 (2.6)	12.9 (1.9)	—	**[a]	17.6 (2.3)	17.2 (2.2)	—	ns	(37)	(52)	
1990	13.6 (2.4)	—	—	—	17.8 (2.2)	—	—	—	(48)		

[a] Bartlett–Box test, $P = 0.048$. Mann-Whitney *U*-test, $Z = -2.58$, $P = 0.0098$.

TABLE 4. Mean values (X) and standard deviation (X) of back-calculated lengths at the first winter (RW1, cm) and at smolting (S), and sample sizes for adult salmon of the river Narcea. Significance of F-tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, nonsignificant. If not indicated, variances were homogeneous (Bartlett-Box F-test, $P > 0.05$).

	RW1				S						
Smolt	1.1	1.2	1.3		1 1	1.2	1.3			N	
year	X SD	X SD	X SD	P	X SD	X SD	X SD	P	(1.1)	(1.2)	(1.3)
1982	—	—	12.0 (2.5)	—	—	—	15.7 (2.1)	—			(54)
1983	—	11.1 (2.7)	—	—	—	14.9 (2.2)	—	—		(28)	
1984	15.7 (1.5)	—	13.8 (2.5)	ns[b]	17.4 (1.6)	—	15.7 (2.1)	ns[b]	(8)		(17)
1985	—	12.8(2.0)	13.0 (3.9)	ns[a]	—	15.8 (1.8)	16.1 (2.7)	ns		(134)	(7)
1986	13.6 (2.5)	15.0 (2.3)	15.0 (1.8)	***	16.1 (2.2)	17.2 (1.9)	17.0 (2.0)	***	(126)	(85)	(17)
1987	13.4 (2.8)	14.8 (2.7)	8.5	**	17.3 (2.4)	18.4 (2.4)	12.6	*	(76)	(51)	(1)
1988	15.0 (1.6)	13.2 (2.4)	12.9	ns	17.3 (1.2)	16.8 (2.0)	17.1	ns	(6)	(75)	(2)
1989	15.1 (2.1)	14.7 (1.9)	—	ns	18.1 (1.8)	18.0 (1.8)	—	ns	(58)	(68)	
1990	13.7 (2.6)	—	—	—	18.2 (2.1)	—	—	—	(51)		

[a] Bartlett–Box test, $P = 0.005$. Mann-Whitney U-test, $Z = -0.826$, $P = 0.409$.

[b] $0.05 < P < 0.06$.

At their first winter, river age 1 salmon from the Esva, Cares, and Narcea rivers (smolt years pooled) formed unimodal length-frequency distributions with modes between 12 and 14 cm (Fig. 4). In all three subsets there was a relatively large group of fish without spring growth (1° smolts; Fig. 5). These fish were significantly larger at RW1 than smolts with spring growth, but were symmetrically included in the size distributions of 1^+ smolts (Fig. 4). In fact, the length-frequency distributions of 1° and 1^+ smolts had a common modal class in the Narcea (17 cm) and Esva (16 cm) rivers. Age 2 smolts were larger (overall mean) than age 1 smolts in the Narcea (18.3 versus 16.8 cm; *t*-test, $P < 0.001$), Esva (16.4 versus 15.1 cm; $P < 0.001$), and Cares rivers (19.6 versus 16.9 cm; $P < 0.001$).

Two-way ANOVA (three rivers × four smolt-years, restrained to age 1.2) revealed significant differences in S among rivers ($F_{2,588} = 93.41$, $P < 0.001$) (Fig. 6) and among years ($F_{3,588} = 3.34$, $P < 0.05$). Variation among rivers was greater than variation among years within rivers. Furtherly, we performed separate one-way ANOVA for each river; interannual variation in *S* was significant for the Narcea and Cares rivers ($P = 0.0003$ and $P = 0.0159$), but not for the Esva River ($P > 0.25$). Variation in mean *S* was less pronounced than in RW1. Changes in mean *S* were correlated in the Narcea and Cares rivers ($r = 0.914$, $P < 0.05$; $n = 5$), but not between the Esva and either of the other two rivers (*r* values: 0.446, and 0.578, $P > 0.05$). There were no significant correlations among rivers for RW1 (*r* values: 0.438, 0.682, and 0.498, $P > 0.05$). Both RW1 and S were larger in the Narcea and Cares than in the Esva River. Almost all smolts belong to the age-classes 1 or 2, being age 3 smolts less than 0.05% of juvenile and adult samples. Most salmon smoltify at age 1, but there are differences between stocks (Fig. 7). In the Narcea River, the proportion of river age 1 salmon ranged from 85 to 99% among years (1985 and 1987–91). This range was from 74 to 96% for the Cares River (1988–91), and from 54 to 90% for the Esva River (1984 and 1987–91).

There were highly significant positive correlations between RW1 and S for each river and smolt year cell, but RW1 and SG were negatively and

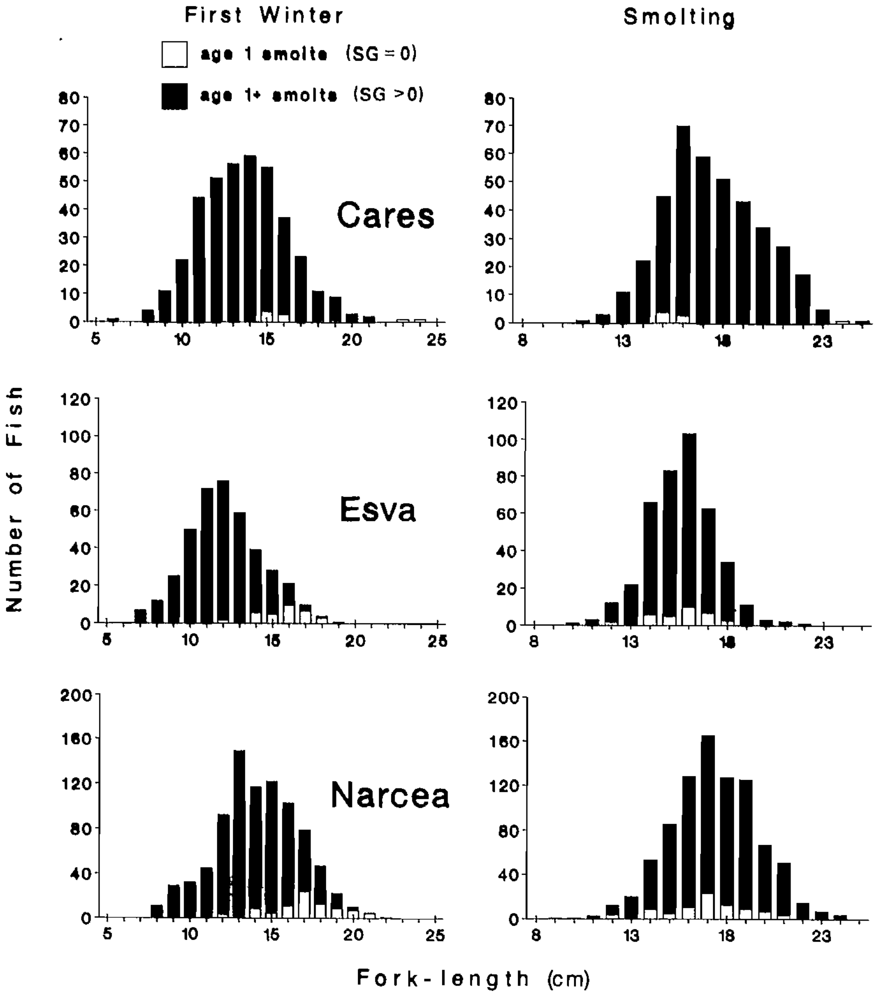

FIG. 4. Frequency distributions of back-calculated lengths (cm) at the first winter (RW1) and smolting (S) for previous 1° and 1+ smolts from rivers Cares, Esva, and Narcea for smolt years 1982–90.

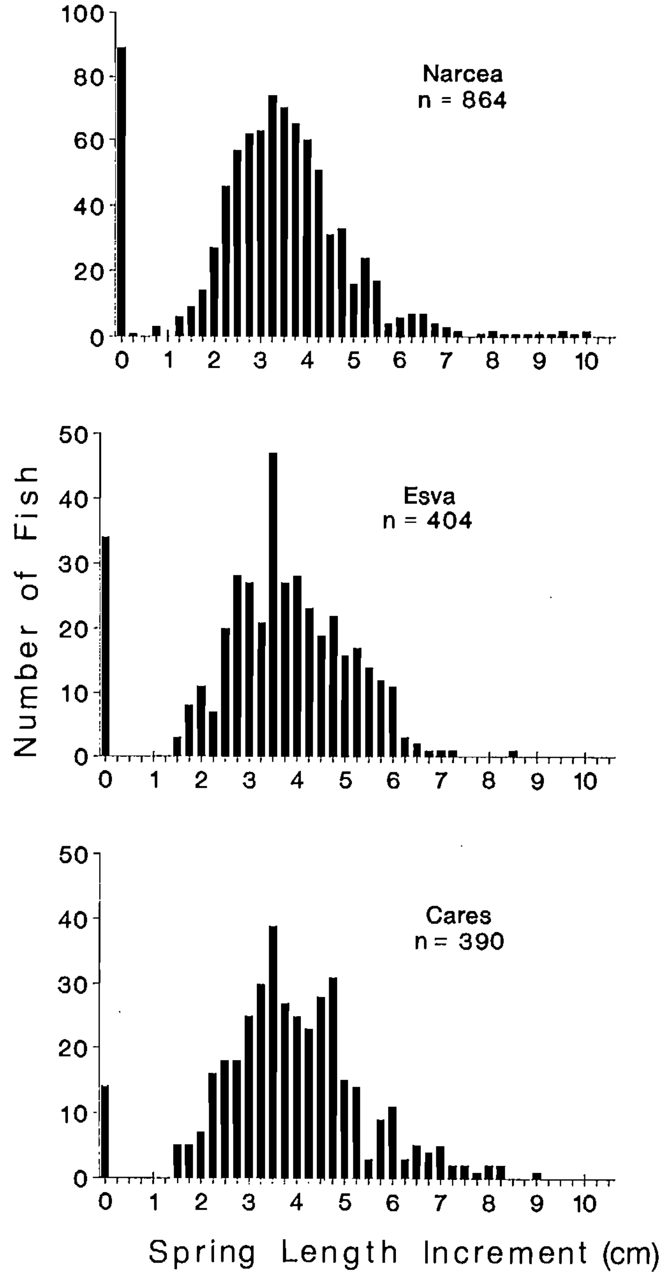

FIG. 5. Frequency distributions of spring body-length increment (cm) of previous age 1 smolts from rivers Cares, Esva, and Narcea for smolt years 1982–90.

significantly correlated in all except one (Cares/1986; Table 5). 1° smolts were excluded from these analyses. RW1 explained about 60–80% of variance in smolt size. By contrast, regressions among SG and S were generally non-significant. As deducted from tables 2 to 4, coefficients of variation of RW1 were consistently higher than those of S, for each river, sea age, and smolt year (Wilcoxon's signed-ranks test, $P < 0.0001$, $n = 34$). For the same samples (1° smolts included), the coefficients of variation of SG ranged from 15% to 72%. Finally, the percentage (arcsine transformation) of 1° smolts was negatively correlated with SG of 1^+ smolts ($r = -0.622$, $P = 0.0034$, $n = 20$).

There was a significant negative correlation between discharge from October to December (D2) and RW1 in all the three rivers (Table 6). Temperature variables associated to the first year in freshwater neither were correlated to growth for any of these rivers. Summer discharge (D1) was positively related to RW1 only for the Narcea. Spring temperatures (T8) were positively correlated to SG for only the Narcea River (Table 6). For the Cares, SG decreased significantly with increasing spring discharge, and specially with March discharge (D7). For the Narcea, no significant correlations were found, but coefficients for discharge variables were negative and relatively high (except D4). No trends were noted for the Esva River.

Discussion

This study provides evidence for the existence of an optimum size at smolting. In all three rivers, the largest fish in winter had the lowest length increments the following spring. There was significant annual variation in smolt size in the Narcea and Cares rivers, so that smolt size was not strictly fixed. Smolt age neither was fixed. However, compensatory growth during the period preceding seaward migration suggests that smolting is 'actively' restricted to a length range that presumably confers survival advantage during the early marine life. In an earlier paper, Nicieza et al. (1991) showed growth bimodality in 0^+ juvenile salmon from rivers Narcea and Esva; furthermore, the fish belonging to the upper modal group (UMG) leave their growth areas after the attainment of a size between 13 and 14 cm. The present results validate this schedule. Most fish having from 14 to 18 cm in the first winter did not show spring growth in their scales. By late January, it is possible to identify on the scales one or two rings corresponding to the second growth period in most UMG fish from the Narcea River system (authors, unpubl. data). Therefore, the break observed in the frequency distributions of SG (Fig. 4) might result from the existence of two kinds of smolts on the basis of the migration timing: late winter smolts (1°, SG = 0), and spring smolts (1^+, SG > 0). The former could have migrated two or three months before other ones of the same age-class (Nicieza et al. 1991). In our study growth compensation does not necessarily imply differences in growth rates because the period during which the riverine spring growth occurrs is highly variable.

The consistency of smolt size over the run has been noted in other rivers (Hesthagen and Garnås 1984). A different pattern in which earlier smolts are larger than later smolts has been often described for wild (Baglinière 1976a; Jonsson et al. 1990) and hatchery-reared stocks (Hansen and Jonsson 1985; Hansen et al. 1989). The length decrease reported in these studies appears to be an effect of non-random sampling of stock mixtures (Chadwick 1987) and declining smolt-age during the spring run, rather than a reduction of mean length within each age-class.

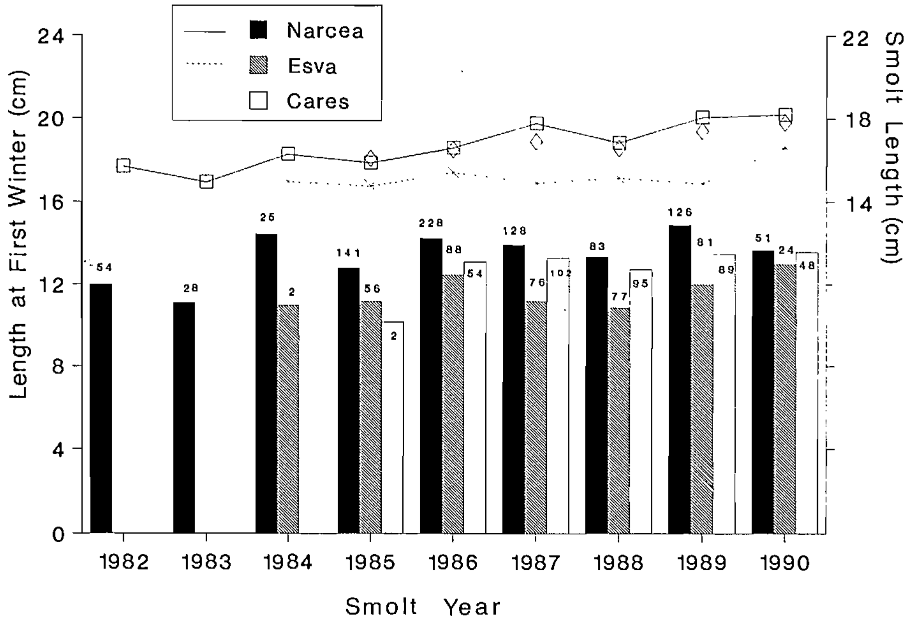

FIG. 6. Mean back-calculated length at first winter (RW1, bars) and at smolting (S, lines) for each smolt year and river (all sea ages combined). Numbers on bars indicate sample size.

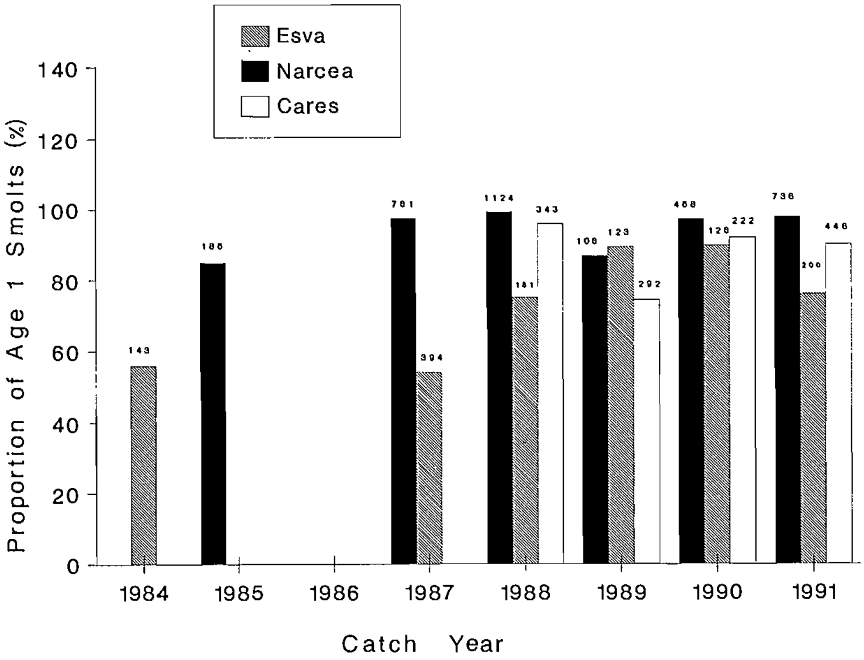

FIG. 7. Percent of smolt age 1 among adult salmon caught by angling in the rivers Narcea, Esva, and Cares over the period 1984–91. Numbers on bars indicate sample size.

Growth (RW1) and smolt size were significantly greater for the Narcea and Cares stocks than for the Esva (Fig. 6). The decreasing arrangement noted for RW1 and S (Narcea > Cares >> Esva) coincides directly with the proportion of fish smolting at age 1°/1⁺ (Fig. 7). In turn, the percentage of 1° smolts increases as the average extent of SG in 1⁺ smolts decreases, indicating a close relationship between growth intensity and smolting patterns. Body size is an important determinant of survival and growth rates of post-smolts (Bilton et al. 1982; West and Larkin 1987; Skilbrei 1989; Ward et al. 1989; Holtby et al. 1990; Henderson and Cass 1991). Thus, smolt size could be a stock-specific trait, adaptive to local conditions in the estuary or nearshore (Riddell and Leggett 1981; Larsson 1985; Lundqvist et al 1988), as suggests the high variation between stocks with respect to variation over years within stocks (cf. Baglinière 1976b; Gibson and Côté 1982; Hesthagen and Garnås 1984; Dutil and Coutu 1986; Chadwick 1987). However, the existence of differences in smolt length between neighbouring stocks, which probably would be subject to similar environmental constraints, is hardly justifiable by local variations in ocean or

TABLE 5. Coefficients of Pearson correlation between back-calculated lengths at first winter (RW1), smolt size (S), and spring size increment (SG) of previous 1^+ smolts. Individuals with SG equal to 0.00 were not included in the analyses (see text); *N*, sample sizes. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Narcea				Esva				Cares			
smolt year	RW1-S	SG-S	RW1-S	*N*	RW1-S	SG-S	RW1-S	*N*	RW1-S	SG-S	RW1-S	*N*
1982	0,868***	0,004	-0,493***	51	—	—	—	—	—	—	—	—
1983	0,841***	−0,068	−0,596***	28	—	—	—	—	—	—	—	—
1984	0,818***	−0,044	−0,610**	16	—	—	—	—	—	—	—	—
1985	0,785***	0,288***	−0,367***	132	0,651***	0,177	−0,631***	50	—	—	—	—
1986	0,888***	0,139	−0,331***	186	0,885***	−0,136	−0,582***	79	0,874***	0,291*	−0,211	51
1987	0,846***	0,019	−0,517***	114	0,746***	0,094	−0,592***	69	0,867***	0,182	−0,333***	97
1988	0,897***	−0,025	−0,464***	79	0,867***	0,188	−0,326**	77	0,852***	0,280**	−0,264**	92
1989	0,859***	0,120	−0,406***	118	0,835***	0,222	−0,350**	69	0,803***	0,323**	−0,303**	88
1990	0,767***	0,055	−0,598***	51	0,866***	−0,250	−0,700***	24	0,845***	0,136	−0,414**	46
Total	0,843***	0,147***	−0,407***	775	0,819***	0,041	−0,539***	370	0,847***	0,257***	−0,293***	376

TABLE 6. Correlation coefficients (r) and significance levels (p) from Pearson correlations between discharge and temperature and growth variables (RW1, SG). D1–D8 are total discharges in different time intervals related to RW1 and SG: D1, July–September; D2, October–December; D3, February–March; D4, December; D5, January; D6, February; D7, March; D8, April. T1–T9 are monthly mean temperatures or sum of means in the interval indicated: T1, March–December; T2, March–July; T3, July–December; T4, October–December; T5, November–December; T6, December–January; T7, February; T8, March; T9, April.

		Narcea ($N = 9$)		Esva ($N = 6$)		Cares ($N = 5$)	
		r	P	r	P	r	P
RW1							
	D1	0,825	= 0,006	−0,014	> 0.1	−0,049	> 0.1
	D2	−0,853	= 0,004	−0,899	= 0,014	−0,812	= 0,094
	T1	−0.059	>0.1	0,654	>0.1	0,339	>0.1
	T2	−0,220	> 0.1	0,693	> 0.1	0,448	> 0.1
	T3	0,131	> 0.1	0,755	= 0,082	0,373	> 0.1
	T4	0,132	> 0.1	0,738	= 0,094	0,401	> 0.1
	T5	−0,089	> 0.1	0,449	> 0.1	0,200	> 0.1
	T6	−0,239	> 0.1	0,313	> 0.1	−0,496	> 0.1
SG							
	D3	−0,566	> 0.1	−0,124	> 0.1	−0,940	= 0,018
	D4	0,416	> 0.1	0,670	> 0.1	−0,016	> 0.1
	D5	−0,616	= 0,078	0,144	> 0.1	−0,825	= 0,086
	D6	−0,542	> 0.1	−0,236	> 0.1	−0,863	= 0,060
	D7	−0,405	> 0.1	0,170	> 0.1	−0,918	= 0,028
	D8	0,017	> 0.1	0,374	> 0.1	0,763	> 0.1
	T7	0,627	= 0,069	0,223	> 0.1	0,361	> 0.1
	T8	0,783	= 0,012	−0,180	> 0.1	0,411	> 0.1
	T9	−0,107	> 0.1	0,667	> 0.1	0,110	> 0.1

estuarine conditions. Rather it may result from differences affecting stream productivity; the Narcea and Cares rivers are located on calcareous watersheds, and their water conductivity and concentration of calcium, phosphate, and nitrate were twice as high (data supplied by the Confederación Hidrográfica del Norte de España) as in the Esva River, which runs over a siliceous watershed. Annual rhythms in seawater adaptation can restrict the time of smolting (Eriksson and Lundqvist 1982; Lundqvist and Eriksson 1985; Hansen and Jonsson 1989), limiting the 'available time' to increase size before seaward migration. If growth rates of juvenile salmon from the Esva are low during the first year, they will be probably low up to smolting time. Therefore, we would expect that, on average, Esva smolts were smaller or later migrants (or both) than Narcea and Cares rivers smolts. For Baltic salmon, Lundqvist et al. (1988) found that smolts in the 18–19 cm length interval had the highest growth rates in the sea. This range is close to the overall mean lengths of age 1 smolts from the Narcea and Cares rivers. Our results indicate that, in the Esva River, less favourable conditions for growth reduce the proportion of fish reaching an optimum smolt size in their first year. Even so, it could be more advantageous for some of these fish to smoltify before they reach the optimum size than delay migration, with the subsequent increase in the generation time, and losses resulting from mortality associated with remaining in freshwater for an additional year. This is consistent with the lower proportion of age 1 smolts and smaller smolt size noted for the Esva River.

For growth during the first year, the strongest and most consistent (negative) correlate was the autumnal discharge (D2). Riddell and Leggett (1981) found the same effect in Canadian rivers, and attributed it to increased costs to hold station. High flow levels reduce the time of foraging and the efficiency of prey capture (Godin and Rangeley 1989). We were unable to detect consistent responses of growth to other environmental variables. It was probably due to limitations established by the reduced sample sizes. In addition, air temperature measurements might not be fine enough as descriptors of water temperatures to account for growth variation. Longer time series and precise estimates of these and other environmental variables are needful to explain within-rivers variations in growth.

In Atlantic salmon, the parr-smolt transformation is coupled with the development of a bimodal growth pattern during the first growing period (see, for review, Thorpe 1987). Although it is yet unclear whether there is a threshold-size to enter the upper modal group (see Wright et al. 1990; Skilbrei 1991), it has been recognized that juvenile salmon must reach a minimum length (about 12–13 cm) to smoltify. The development of growth bimodality might be a filtering mechanism that prevents a number of fish smoltifying below this critical length. In this sense, the existence of bimodality can absorb part of the variability in smolt size caused by environmental factors, while the extent of spring freshwater growth might be a result from some trade-off between size and time of migration. A similar situation has been observed for juvenile sea trout, where the importance of smolt migration is positively correlated with spring growth (Fahy 1990). Compensatory spring growth may be an adaptive mechanism in anadromous salmonids. The observation of a similar relationship during the marine phase (Skilbrei 1990) suggests that it could be a more widespread phenomenon, extensive to other life stages and to non-anadromous forms.

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Comparison of Juvenile Atlantic Salmon (*Salmo salar*) Reared in a Hatchery and Introduced into a Stream: A Two-Size-Threshold Model of Smoltification

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WHITESEL, T. A. 1993. Comparison of juvenile Atlantic salmon (*Salmo salar*) reared in a hatchery and introduced into a steam: a two-size-threshold model of smoltification, p. 239–247. *In* R. J. Gibson and R. E. Cutting [ed.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

This study compared Atlantic salmon reared in a hatchery with fish introduced into a stream and allowed to exist naturally. Atlantic salmon that were introduced into the stream as 8-mo-old parr during October migrated downstream as smolts (silvery without parr marks; condition factor (CF) = 0.95; gill Na^+/K^+ ATPase activity (ATP) = 24 µM Pi·mg protein^{-1}·h^{-1}; ability to survive a salinity tolerance test (STT) = 0%) in early April and generally had a fork length > 110 mm. In contrast, salmon shorter than 110 mm typically did not migrate and retained their parr-like characteristics (golden with parr marks; CF = 1.05; ATP = 8 µM Pi·mg protein^{-1}·h^{-1}; STT = 0%). Salmon that migrated as smolts (CF = 1.03; ATP = 52 µM Pi·mg protein^{-1}·h^{-1}; STT = 0%) after they were introduced into the stream as 14-mo-old fish during April were typically longer than 135 mm and longer than those that remained as stream residents. Both secondary upper and lower mode hatchery salmon also exhibited smolt characteristics (CF depressed; ATP = 55–70 µM Pi·mg protein^{-1}·h^{-1}; STT 33–83%) in early May, if they were > 135 mm in fork length and in the portion of the population that was growing most rapidly. It was also evident that juvenile Atlantic salmon are able to make the physiological decision to smoltify at least as late as February of the spring they will migrate.

La présente étude a permis de comparer des saumons élevés en pisciculture à des poissons introduits dans un cours d'eau pour y grandir de façon naturelle. Les saumons atlantiques introduits en octobre dans la rivière à l'état de tacons de 8 mois ont dévalé à l'état de smolts (livrée argentée sans marques de tacon; facteur de condition (CF) = 0,95; activité de la Na^+/K^+ ATPase dans les branchies (ATP) = 24 µM Pi·mg de protéine $^{-1}$·h^{-1}; aptitude à survivre à un test de tolérance de la salinité (STT) = 0 %) au début d'avril, et ils présentaient dans l'ensemble une longueur à la fourche supérieure à 110 mm. Par contre, les saumons mesurant moins de 110 mm ne migraient en général pas et gardaient leurs caractéristiques de tacon (livrée dorée avec marques de tacon; CF = 1,05; ATP = 8 µM Pi·mg de protéine^{-1}·h^{-1}; STT = 0 %). Les saumons qui migraient à l'état de smolts (CF = 1,03; ATP = 52 µM Pi·mg de protéine $^{-1}$·h^{-1}; STT = 0 %) après avoir été introduits dans la rivière en avril à l'âge de 14 mois mesuraient en général plus de 135 mm et étaient plus longs que ceux qui avaient résidé dans le cours d'eau. Les saumons d'élevage de mode secondaire inférieur et supérieur présentaient aussi des caractéristiques de smolt (baisse du CF; ATP = 55-70 µM Pi·mg de protéine $^{-1}$·h^{-1}; STT = 33-83 %) au début de mai, s'ils mesuraient plus de 135 mm de longueur à la fourche et s'ils se situaient dans la portion de la population qui connaissait la croissance la plus rapide. Il était aussi évident que les jeunes saumons atlantiques étaient capables de prendre la décision physiologique de la smoltification au moins jusqu'en février pour migrer au printemps.

Introduction

The development of hatchery-reared Atlantic salmon juveniles, once placed into streams, has not been well explored. Atlantic salmon whose early growth has been accelerated may demonstrate the morphological characteristics of a smolt yet fail to grow substantially for the first 6–12 months after transfer to sea cages (Saunders et al. 1985). When Atlantic salmon are stocked as smolts, many may fail to migrate down streams (Wedemeyer et al. 1980; Loyenko and Chernitsky 1984; Whitesel 1990) or through lakes (Hansen et al. 1984) to the ocean. These complications, combined with the genetic mixing of stocks and relatively little information on natural smolt development, make it difficult to determine the stage of development at which it is most appropriate to stock juvenile salmonids from a hatchery into the wild.

Smoltification is the sequence of changes associated with the transformation of juvenile salmonids from freshwater resident parr to seaward-bound smolts (Schreck 1982). Smolts have been defined in physiological, behavioral and morphological terms (reviewed by Hoar 1988). Atlantic salmon parr must enter the UMG and reach a critical length before they have the potential to smoltify (Elson 1957; Thorpe et al. 1980; Kristinsson et al. 1985). Smolts typically exhibit a decrease in their condition factor (Hoar 1939) and undergo a well-defined migration to the ocean (White 1939; Allen 1944; Osterdahl 1969). Finally, a functional smolt will have elevated gill Na^+/K^+ ATPase

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activity (Boeuf and Prunet 1985; McCormick et al. 1987) and survive a transition to seawater (Johnston and Saunders 1981; Saunders et al. 1985).

A bimodal length-frequency distribution is common in wild and hatchery-reared juvenile salmon when growth conditions are good during their first year (Bagliniere and Maisse 1985; Clarke and Shelbourn 1986; Hirata et al. 1988; Metcalfe et al. 1988; Nicieza et al. 1991). In hatchery-reared Atlantic salmon the divergence between the two modes of growth becomes evident during late summer and early fall (Bailey et al. 1980; Thorpe et al. 1980) and is the result of rapidly growing parr being recruited into the upper modal group (UMG) (Kristinsson et al. 1985). Upper modal growth salmon generally smoltify in the spring of their second year whereas parr from the lower modal group (LMG) defer smoltification for an extra year (Thorpe 1977; Bailey et al. 1980). It is not clear when the life-history patterns of the parr are determined (Kristinsson et al. 1985; Skilbrei 1988; Stefansson et al. 1989; Stewart et al. 1990), although the modal structure (Thorpe 1989) and the decision to smoltify (Elson 1957) are often considered to be fixed by the first fall.

Examination of the natural process of smoltification is necessary to understand better the contribution hatchery-reared fish make to smolt production in the riverine environment. Labor-intensive experiments have begun to compare naturally produced and hatchery-reared Atlantic salmon juveniles (Piggins and Mills 1985; Virtanen and Soivio 1985). These studies present evidence which suggests that smolts in their natural environment develop differently than fish in captivity. However, experiments which rigorously compare the development of hatchery-reared and naturally existing salmon from the same cohort (Whitesel 1987; 1990) are rare. Thus, the objectives of this study were to compare the development of juvenile Atlantic salmon in their natural environment to that of fish from the same cohort reared in a captive environment. In addition, an attempt was made to evaluate whether critical length models are indicative of the natural process of smoltification.

Methods and Materials

Atlantic salmon embryos (ultimately of Penobscot River (Maine, USA) origin and the offspring of Union River (Maine, USA) Atlantic salmon that had been reared in captivity for one year) at the North Attleboro National Fish Hatchery (Massachusetts, USA) hatched in January and February and began to feed in April, 1988. They were transferred into 2.5-m-wide by 1.5-m-deep concrete raceways during July and August and held at a density of ca. 6 g·L^{-1}. In the raceways fish were fed U.S. Fish and Wildlife Service ASD 2–30 salmon feed at 2% body weight·day^{-1} over eight feeding periods.

Juvenile Atlantic salmon were reared in the hatchery and introduced into a stream in the fall prior to and in the spring during which they would have smoltified as 1-yr-old fish. The developmental process of fish in the stream was compared to that of fish in the hatchery. Migrating fish were also compared to stream dwelling, non-migrants during the same period of time. Atlantic salmon from each environment were generally sampled once each month during the winter, twice each month during March and April, and four times in May. Atlantic salmon from the hatchery were netted from the raceway and anaesthetized in 0.3% 2-phenoxyethanol. Before being anaesthetized, stream-resident salmon were captured by electrofishing while migrants were captured downstream of the stocking sites with a modified fyke net attached to a holding box. The trap was installed during mid-March and monitored daily through the beginning of June. Capture did not affect any of the parameters being investigated (Whitesel 1987, 1990).

In October, 1988, these fish were graded (≤ or > 95 mm fork length) such that the UMG salmon (mean fork length (MFL) = 103 mm; Fig. 1) were stocked into the Beaver River, Rhode Island (BVRO) (areas 1 and 2, Fig. 2). The remaining salmon from the LMG (MFL = 84 mm) were kept in the hatchery. As part of the routine hatchery practice designed to improve growth conditions for smaller fish, the salmon remaining in the hatchery were further separated by fork length (≤ or > 105 mm) in February, 1989. This resulted in the development of two different modal sizes of growth in the hatchery. Thus, salmon in secondary modes of growth (2°−UMG and 2°−LMG) were sampled at the hatchery from March through the end of May (Fig. 1). In April, 1989, 14 mo. old 2°−UMG Atlantic salmon (BVRA; MFL = 175 mm; Fig. 1) were also introduced into the BVR (area 3, Fig. 2). The fish were given various fin-clips so that each group was distinguishable. No effect of fin-clipping was observed on migration or swimming ability.

Salmon in the hatchery were held under a natural photoperiod in flow-through water that remained near 10°C until mid-May (1989) when, for management purposes, they were moved into an alternate holding area with 15°C water for the remainder of the experiment (Fig. 3). The water temperature of BVR ranged from 0.5°C in February to 18°C in June (Fig. 3). The water depth and the rate at which water entered the raceways at the hatchery remained relatively constant. From 17 March until 3 June the relative depth of BVR ranged from 39.5 cm on 18 March to 92.0 cm on 11 May (Fig. 3). The amount of rainfall during this period ranged from 0.0 cm on numerous days to 4.0 cm on 11 May (Fig. 3). However, neither the depth nor rain guage was operational during flooding from 16 to 19 April. The fork length and weight of each fish were measured, their physical appearance (i.e. presence or absence of parr marks) was noted and their condition factor calculated as weight(cg)·(fork length(cm)^3)$^{-1}$. Fork length and length-frequency distributions were used to evaluate the size and growth characteristics of the salmon.

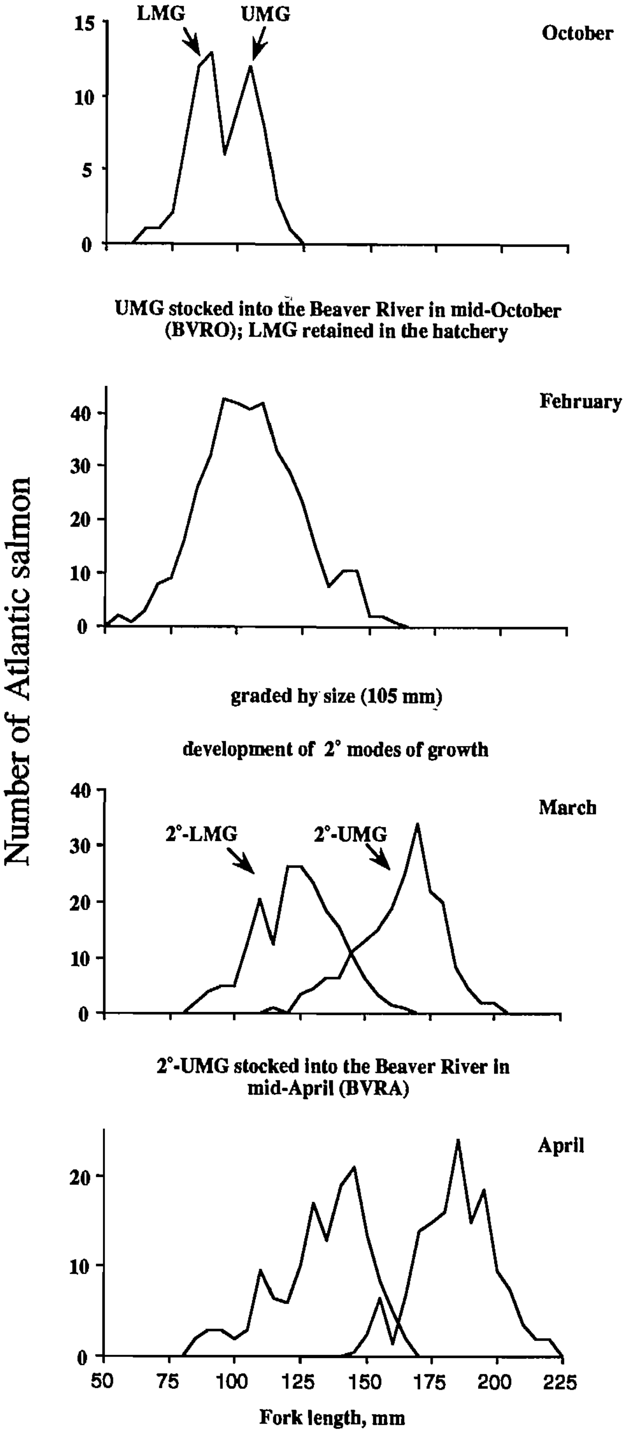

FIG. 1. Length-frequency distributions of Alantic salmon reared at North Attleboro Fish Hatchery. Two modes of growth were evident statistically in October, 1988 (n=75). Fish from the UMG were stocked into the Beaver River (BVRO) while those in the LMG were kept in the hatchery. On 2 February, 1989, the salmon (n=300) were graded into size classes ≥ or < 105 mm. As a result of this grading, the fish developed as secondary modal groups (2°–UMG and 2°–LMG) (see 31 March and 29 April, 1989; n=150 per group). In mid-April, 1989, some of the 2° –UMG fish were stocked into the Beaver River (BVRA).

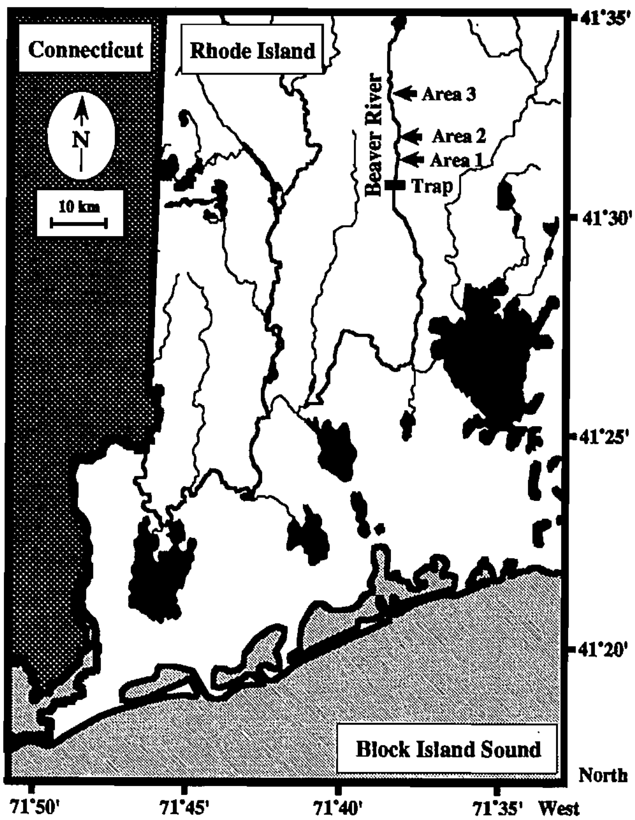

FIG. 2. Location of the Beaver River study area, Washington county, Rhode Island. Darkened areas in Rhode Island represent fresh water while swamps are indicated by stippled areas.

TABLE 1. Percent survival of Atlantic salmon subjected to a salinity tolerance test (exposure to a salinity of 40 ppt for 72 h). 2°–LMG; secondary lower modal group fish from North Attleboro Fish Hatchery: 2°–UMG; secondary upper modal group fish from North Attleboro Fish Hatchery: BVRO; fish stocked into the Beaver River in October, 1988: BVRA; fish stocked into the Beaver River in April, 1989, that remained as stream residents. (^T = increased length (> 36 h) of survival). No mortality occurred in control fish transferred to fresh water.

	North Attleboro Fish Hatchery		Beaver River	
Date	2°–LMG	2°–UMG	BVRO	BVRA
21FEB89	0			
20MAR89			0	
29MAR89	0	0		
13APR89	0	0		
18APR89			0	
28APR89	0	0(^T)		
30APR89				0
4MAY89	0(^T)	17	0	
11MAY89	33	83		
18MAY89	0	0	0	

Osmoregulatory ability was assessed by challenging the salmon in a salinity tolerance test modified from Johnston and Saunders (1981) and Saunders et al. (1985) (see Table 1). The test consisted of a 72 h challenge in a salinity of 40 ppt and a temperature of 10°C (Whitesel 1990). Branchial Na$^+$/K$^+$ ATPase activity was also measured. Gill filaments were excised from fish, rinsed in a sucrose-EDTA-imidazole (SEI) buffer (Zaugg 1982), placed in vials containing SEI buffer, rapidly frozen on dry ice and stored at -80°C. Gills were homogenized, enzymes liberated in a SEI-deoxycholate solution and Na$^+$/K$^+$ ATPase activity measured using a colorimetric assay (Bradley et al. 1989). Final activity is expressed as µM Pi·mg protein^{-1}·h^{-1}. Inter- and intra-assay coefficients of variation were 9 and 7%, respectively.

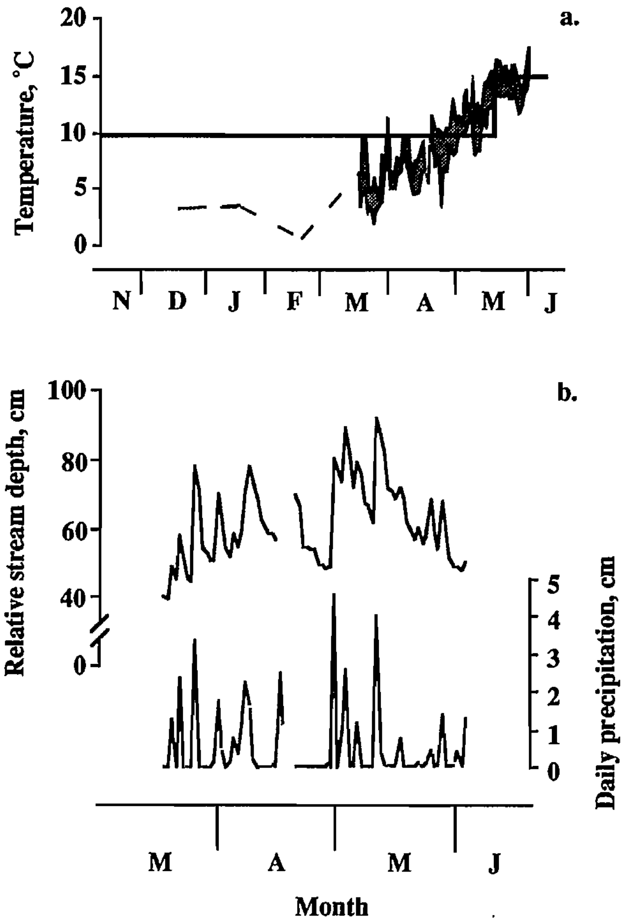

FIG. 3. (a) Water temperature regimes at North Attleboro Fish Hatchery (bold line) and the Beaver River (broken line), November 1988–June 1989. The daily range in temperature of the Beaver River (stippled area) is indicated from 17 March–3 June. (b) Relative stream depth and daily precipitation at the Beaver River trap site. Data were not collected from 16–19 April because of flooding.

Means were analyzed by Student's *t*-test or one-way ANOVA followed by Student-Newman-Keuls (SNK) multiple comparison test. Significant differences were accepted when $P \le 0.05$.

Results

Hatchery

2°−UMG. Mean condition factor of the 2°−UMG declined from 1.10 in March to a low of 0.95 in early May, after which it remained depressed (Fig. 4). Salinity tolerance began to improve on 28 April, peaked at 83% survival on 11 May and exhibited 0% survival thereafter (Table 1). Mean gill Na^+/K^+ ATPase activity increased nearly five-fold, from 10 µM Pi·mg protein^{-1}·h^{-1} in February to between 40 and 65 µM Pi·mg protein^{-1}·h^{-1} in March and April (Fig 5). Mean gill Na^+/K^+ ATPase activity peaked at 72 µM Pi·mg protein^{-1}·h^{-1} in early May, decreased to 23 µM Pi·mg protein^{-1}·h^{-1} by the middle of May and remained low afterwards (Fig. 5). Mean fork length of the 2°–UMG fish increased from 150 mm in March to a plateau near 190 mm during May and June (Fig. 6). At the end of April approximately 83% of 2°−UMG salmon were longer than 160 mm (Fig. 1). 2°−UMG salmon that exhibited smolt-like characteristics (i.e., increased gill Na^+/K^+ ATPase activity, decreased condition factor) at the end of April and beginning of May tended to be longer than 160 mm while those that retained their parr-like characteristics were generally shorter than 160 mm.

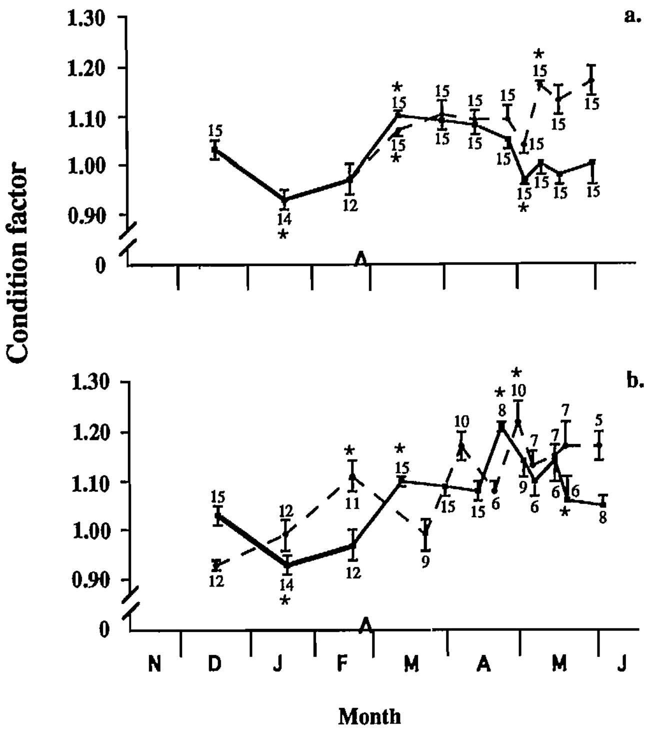

FIG. 4. (a) Condition factor of juvenile Atlantic salmon sampled from North Attleboro Fish Hatchery prior to grading in February (bold line), 2°−UMG (solid line) and 2°−LMG (broken line). (b) Condition factor of juvenile Atlantic salmon stocked into the Beaver River in October, 1988 (BVRO; broken line) and April, 1989 (BVRA; solid line).
Values are expressed as the Mean ± SE. * indicates a significant change over time within a group of fish. ^ indicates the date when salmon in the hatchery were separated into the secondary modal groups.

2°−LMG. The mean condition factor of the 2°−LMG salmon remained near 1.10 during March and April then increased to a plateau near 1.15 in May where it remained for the rest of the study (Fig. 4). Salinity tolerance increased from 0% survival on 4 May to 33% survival on 11 May and 0% survival therafter (Table 1). Mean gill Na^+/K^+ ATPase activity was 10 µM Pi·mg protein^{-1}·h^{-1} in February, increased five-fold by early March, peaking at 57 µM Pi·mg protein^{-1}·h^{-1} in the beginning of May and then decreasing to baseline activity by the end of May (Fig. 5). The mean fork length of the 2°−LMG increased from 120 mm in the beginning of April to 150 mm in May (Fig. 6). At the end of April approximately 75% of these salmon were larger than 120 mm (Fig. 1). The majority of the 2°−LMG salmon that exhibited smolt-like characteristics were longer than 135 mm whereas those that retained their parr-like characteristics were generally shorter than 135 mm.

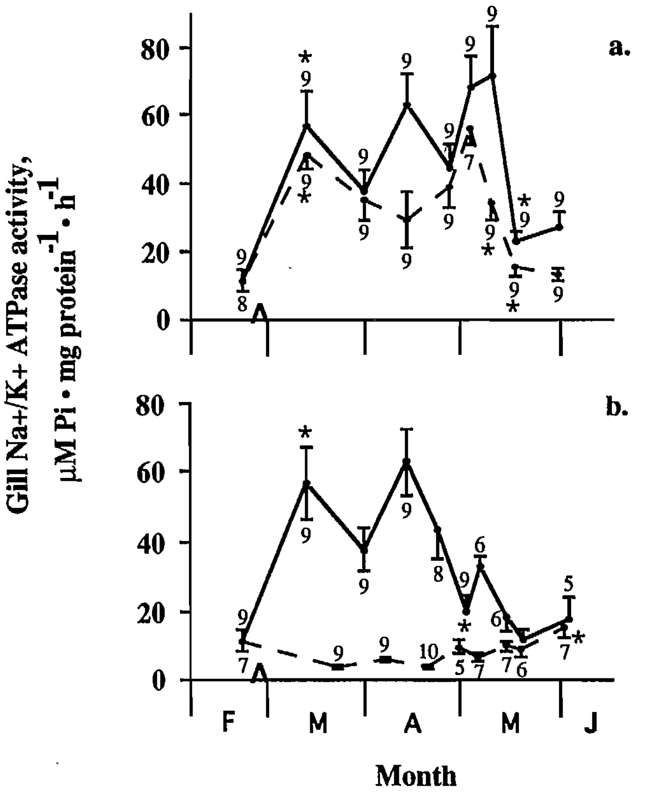

FIG. 5. (a) Gill Na+/K+ ATPase activity of juvenile Atlantic salmon sampled from North Attleboro Fish Hatchery prior to grading in February (bold line), 2°−UMG (solid line) and 2°−LMG (broken line). (b) Gill Na+/K+ ATPase activity of juvenile Atlantic salmon stocked into the Beaver River in October, 1988 (BVRO; broken line) and April, 1989 (BVRA; solid line). Values are expressed as the Mean ± SE. * indicates a significant change over time within a group of fish. ^ indicates the date when salmon in the hatchery were separated into the secondary modal groups.

Beaver River

BVRO. Although somewhat variable, the mean condition factor of stream resident BVRO salmon generally increased during the course of the study ranging from 0.93 in December to 1.22 at the beginning of May (Fig. 4). These salmon never survived in a salinity tolerance test (Table 1). Mean gill Na+/K+ ATPase activity in the gills of these salmon remained between 4 and 11 µM Pi·mg protein^{-1}·h^{-1} for most of the investigation and increased to only 15 µM Pi·mg protein^{-1}·h^{-1} in June (Fig. 5). The mean fork length of BVRO stream residents remained near 95 mm, unchanged from December through February (Fig. 6). The mean fork length of these fish increased in March and reached a maximum of 120 mm at the end of the study (Fig. 6).

BVRA. The mean condition factor of the BVRA salmon sampled during April and May, near the area of the stream in which they were stocked (1.21), tended to be greater than that of the original group of fish placed from the hatchery into the stream in April (1.09) (Fig. 4). However, the mean condition factor of stream resident fish decreased to 1.08 after less than 1 mo. of stream residence (Fig. 4). On 30 April stream resident BVRA fish captured near area 3 of the river did not survive in a salinity tolerance test (Table 1). Mean gill Na+/K+ ATPase activity of BVRA residents was near 50 µM Pi·mg protein^{-1}·h^{-1} when the fish were stocked, decreased to 20 µM Pi·mg protein^{-1}·h^{-1} by late April and exhibited no significant change therafter (Fig. 5). The fork length of the stream resident BVRA Atlantic salmon that remained near area 3 of the BVR was consistently around 145 mm, significantly shorter than the average fish stocked into the river (Fig. 6).

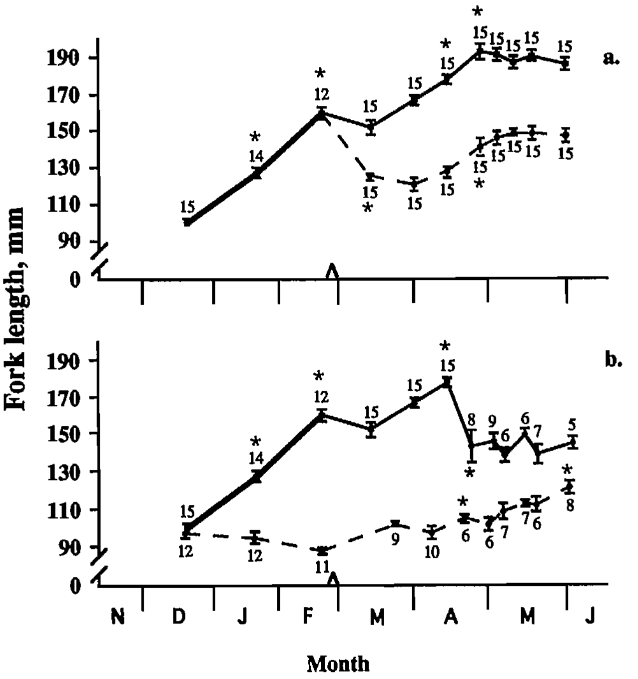

FIG. 6. (a) Fork length of juvenile Atlantic salmon sampled from North Attleboro Fish Hatchery prior to grading in February (bold line), 2°−UMG (solid line) and 2°−LMG (broken line). (b) Fork length of juvenile Atlantic salmon stocked into the Beaver River in October, 1988 (BVRO; broken line) and April, 1989 (BVRA; solid line).
Values are expressed as the Mean ± SE. * indicates a significant change over time within a group of fish. ^ indicates the date when salmon in the hatchery were separated into the secondary modal groups.

Downstream movement

BVRO. All the BVRO migrants were silvery without parr marks whereas only 4% of the stream residents exhibited any signs of silvering (Table 2). The condition factor of migrants (0.95) was significantly lower than that of resident fish (1.09) (Table 2). The mean gill Na+/K+ ATPase activity (24 µM Pi·mg protein^{-1}·h^{-1}) of migrating BVRO Atlantic salmon was greater than that of resident salmon (8 µM Pi·mg protein^{-1}·h^{-1}) captured during the same period of time (Table 2). The fork length of migrating BVRO smolts captured in the trap during this study, along with that of Atlantic salmon in a similar study the previous year (Whitesel 1990), was normally distributed around a mean of 135 mm (Table 2) and

TABLE 2. Pigmentation (expressed as silvering and calculated as the percent of fish without visible parr marks), fork length (FL, mm), condition factor (CF) and gill Na^+/K^+ ATPase activity (ATP, μM Pi·mg $protein^{-1}·h^{-1}$) in juvenile Atlantic salmon sampled from the trap as downstream migrants or from the stream as resident parr during April and May. BVRO; fish stocked into the Beaver River in October, 1988: BVRA; fish stocked into the Beaver River in April, 1989. Characteristics (expressed as the MEAN ± SE, or percentage, with the associated sample size) between capture locations were compared within a group of fish. * indicates a significant difference ($P \leq 0.05$) between salmon sampled from the stream and those sampled from the trap.

Group of fish	Capture location	Characteristic				
		n	silvering	CF	ATP	FL
BVRO	TRAP	6	100%	0.95 ± .01	24 ± 4	135 ± 7
	STREAM	48	4% *	1.09 ± .01 *	8 ± 1 *	102 ± 1 *
BVRA	TRAP	18	no data	1.03 ± .02	52 ± 7	166 ± 3
	STREAM	8	no data	1.14 ± .04 *	28 ± 5 *	143 ± 4 *

ranged from 110 to 160 mm. The BVRO salmon that remained as stream residents during this period of time had a mean fork length of 102 mm (Table 2) and were generally shorter than 110 mm.

BVRA. Scale loss, presumably incurred during transportation, prohibited the quantification of pigmentation of many of the BVRA salmon sampled in the stream. The mean condition factor of BVRA smolts captured in the trap was lower (1.03) than that of resident fish (1.14) sampled during the same time (Table 2). Gill Na^+/K^+ ATPase activity in migrating BVRA salmon (52 μM Pi·mg $protein^{-1}·h^{-1}$) was higher than that of residents (28 μM Pi·mg $protein^{-1}·h^{-1}$) (Table 2). The mean fork length of migrating BVRA Atlantic salmon smolts was longer (166 mm) than that of stream residents BVRA fish (143 mm) sampled during the same respective time period (Table 2). The fork length of the BVRA salmon that did not migrate as smolts when stocked into the river was generally shorter than 160 mm (Fig. 1).

Discussion

Juvenile Atlantic salmon placed into the stream as 8-mo-old parr were able to begin their seaward migration (smoltification) as 14-mo-old fish at fork lengths ranging from 110–155 mm, and approximately 50% of these fish were shorter than 135 mm. This size range is typical for 1-yr-old wild Atlantic salmon smolts (Allen 1944; Piggins and Mills 1985; Cunjak et al. 1990). Since Atlantic salmon smolts feed and grow well during their migration (Allen 1944) it seems reasonable to presume that they may go through a rapid phase of growth and potentially reach the second size threshold prior to ocean residence. Atlantic salmon that have short smolt migrations may achieve the second size threshold by growing in the estuary (Cunjak et al. 1989). Current evidence suggests that wild Atlantic salmon which begin to smoltify and reach a fork length of approximately 135 mm move into the ocean (Nicieza et al. 1991) while those that fail to reach this size may return from the estuary back to the river (Cunjak et al. 1989). Thus, similar to previous studies on hatchery-reared (Kristinsson et al. 1985) and wild (Nicieza et al. 1991) salmon, a size threshold near 110 mm appeared to be required in order for feral salmon to begin the final process of smoltification.

Atlantic salmon juveniles that overwintered in the stream began to exhibit smolt characteristics at a time similar to when the same cohort of salmon appeared to begin smoltification in the hatchery, but before their hatchery counterparts reached peak smolt condition. The strongest indication that feral salmon smoltified was their display of downstream migratory behavior. BVRO salmon captured in the spring, 6 mo after they had been put in the stream, appeared to be migrating as smolts rather than dispersing downstream. Each year the trap was installed during the middle of March to provide a baseline of nearly 14 d during which no Atlantic salmon were captured, suggesting this was a true migration rather than more generalized wandering. The mean timing of the smolt migration during the two years of this study was from 3 April to 12 May. The specific timing of the smolt migration in wild Atlantic salmon varies with latitude; however, the period of movement observed in this study was not atypical (see Youngson et al. 1983; Hansen and Jonsson 1985).

In support of the claim that these migrants were smolts, they also had elevated gill Na^+/K^+ ATPase activity, had a relatively low condition factor and were silvery without any parr marks. However, approximately half of these feral salmon were between 110 and 135 mm and had not reached a size generally considered necessary for smoltification to occur in fish that were originally from a hatchery (Kristinsson et al. 1985). It is possible that these feral Atlantic salmon may have become more like wild than hatchery fish because they were forced to overwinter in the river. In as much as this is true, the similarity in the size of BVRO migrants and wild 1-yr-old Atlantic salmon smolts (Piggins and Mills 1985; Cunjak et al. 1990) is also consistent with the claim that BVRO salmon captured in the trap were beginning a seaward migration. In any event, the majority of the evidence suggests that these migrants represented smolts. Peak smolt condition in feral salmon probably occurred farther downstream since smolt development progresses during the seaward migration (Allen 1944).

Although the exact number of BVRO salmon that smoltified could not be calculated, it was clear that some of the fish put in the stream as parr did not grow enough during the intervening months to smoltify in the spring. The fish that remained in the stream as feral parr had prominent parr marks, yellow fins and, often times, orange spots on their sides. These fish were typically shorter than 110 mm, smaller than those that migrated.

The longest of the 14-mo-old captive Atlantic salmon introduced into the river in April quickly moved downstream. These fish were from the portion of the distribution of the 2°−UMG that had evidently grown or were growing relatively rapidly. Migrant salmon were larger, had a lower condition factor and greater gill Na^+/K^+ ATPase activity than fish which remained at the stocking site. Thus, although a period of dispersal is common immediately after fish are stocked into streams (Cresswell 1981), fish longer than 160 mm appeared to be migrating as smolts.

Some of the BVRA salmon remained in the area where they were stocked and did not migrate as smolts. BVRA Atlantic salmon that did not move downstream quickly developed a condition similar to that of feral parr. Their gill Na^+/K^+ ATPase activity was relatively high in the hatchery during April. However, after 21–28 d in the stream the level of activity had declined and become comparable to that of feral Atlantic salmon parr in the stream. These fish did not smoltify despite being larger (140–160 mm) than what is generally reported as a critical length for smoltification (135 mm) in North American Atlantic salmon (Bailey et al. 1980; Kristinsson et al. 1985). Based on their size, these fish were apparently from the slower-growing portion of the 2°−UMG.

In contrast, despite being in the LMG the preceding fall, hatchery-reared Atlantic salmon from the 2°−UMG underwent changes to suggest that they smoltified as 15 mo. old fish. Juvenile Atlantic salmon that have not been recruited into the UMG by their first autumn are generally expected to remain in the LMG and not smoltify as 15 mo. old fish (Thorpe 1977; Thorpe et al. 1982). However, fish in the present study, originally from the LMG, reached 135 mm in fork length, exhibited their lowest condition factor and highest hypo-osmoregulatory ability during or before May. A peak in the smolt condition of captive Atlantic salmon near the beginning of May is fairly common (McCormick et al. 1987). Thus, in contrast to the ideas of Metcalfe et al. (1988), data from this investigation suggest that salmon from the LMG can smoltify as 15 mo. old fish.

Furthermore, this investigation suggests that 2°−LMG fish could be recruited as smolts well into the spring. The division between North American UMG smolts and LMG parr in the spring has been reported to be near 135 mm (Bailey et al. 1980; Kristinsson et al. 1985; Saunders et al. 1985). The length-frequency distribution of the fish in this study indicated nearly 50% of the 2°−LMG fish were greater than 135 mm by the end of April, by early May gill Na^+/K^+ ATPase activity was relatively high, an estimated 33% were able to survive in a salinity tolerance test and approximately 30% had developed a silvery coloration. Thus, it seemed that potentially one-third to one-half of the 2°−LMG Atlantic salmon had developed enough to begin to smoltify as 15-mo-old fish. These data agree with the findings of Kristinsson et al.(1985), Skilbrei (1988), Stefansson et al. (1989) and Stewart et al. (1990) that LMG Atlantic salmon continue to move into the upper mode of growth at water temperatures of 8–10°C or greater. Captive salmon in the present study never experienced temperatures below 10°C. Thus, it appears that when growing conditions are good the modal structure can be continually modified. In this study Atlantic salmon juveniles entered the smolting portion of the population as late as February, less than 3 mo. prior to the time when they reached peak smolt condition.

It appeared that juvenile Atlantic salmon needed to reach a size of approximately 135 mm in fork length to complete the process of smoltification. This was evident when 2°−LMG fish that did not reach this size, prior to the seasonal end of the smolt period in May, did not appear to smoltify. Evidence exists which suggests that the seasonal end of the smolt period for Atlantic salmon is generally during May and June, dictated in part by elevated water temperatures (Duston et al. 1991). A critical length, or threshold size, for smoltification near 135 mm is in agreement with a number of other studies on North American Atlantic salmon (Elson 1957; Bailey et al. 1980; Kristinsson et al. 1985).

In order to smoltify Atlantic salmon also appear to need to experience a rapid growth phase. Despite being larger than 135 mm at the end of April, an estimated 17% of the 2°–UMG fish never survived a salinity tolerance test and also had prevalent parr marks. Therefore, that portion of the 2°–UMG salmon did not appear to completely smoltify, similar to the findings of Nicieza et al. (1991) who worked with wild Atlantic salmon in Spain. The salmon which exhibited these parr-like characteristics were typically shorter than 160 mm. Correspondingly, 14 mo. old juvenile Atlantic salmon that migrated after being moved from the hatchery to the stream were typically longer than 160 mm. Taken as a whole, this data suggests that the BVRA fish that grew relatively rapidly were those that smoltified. The necessity of a rapid phase of growth to smoltify agrees with studies demonstrating that accelerated growth is the mechanism for recruitment of UMG salmon (Bailey et al. 1980; Kristinsson et al. 1985; Metcalfe et al. 1988) and is involved in the decision to smoltify (Metcalfe and Thorpe 1990; Metcalfe et al. 1990; Nicieza et al. 1991).

In conclusion, the data from this investigation help to emphasize that smoltification is a complex process and suggest that juvenile Atlantic salmon may experience three size-related stages of smolt development. Although critical sizes may be different between strains of Atlantic salmon (Thorpe et al. 1980), captive Atlantic salmon juveniles from North

American stocks appear to move from the LMG into a transitional phase of rapid growth once they reach a threshold fork length of approximately 110 mm (Kristinsson et al. 1985). They seem to leave this transitional phase and enter the UMG at a second threshold size near 135 mm (Bailey et al. 1980; Saunders et al. 1985). The present study suggests that the parr-smolt transformation in Atlantic salmon requires both entering the rapid growth phase and reaching the second size threshold before the end of the smoltification period in May and June. This concept agrees with the ideas that critical length models are adequate first approximations but are too simplistic (Myers et al. 1986; Rowe and Thorpe 1990), and that along with absolute size, growth rate is an important factor in developmental decisions (Thorpe 1986).

A two-size-threshold model may be appropriate for beginning to assess the contribution of hatchery-reared, feral and wild Atlantic salmon to the production of smolts in the natural environment. In this investigation, only feral Atlantic salmon that had reached the first size threshold began to migrate and, therefore, began the final process of smoltification. Thus, in Atlantic salmon, the first size-threshold appears to be related to the initiation of migration as well as final smolt development, while the second size threshold may be more closely related to hypoosmoregulatory ability (McCormick and Saunders 1987) and the completion of smoltification.

Although some decisions concerning smoltification may be made by the salmon in the preceding fall (Elson 1957; Bailey et al. 1980; Thorpe et al. 1980; Kristinsson et al. 1985) this investigation supports the hypothesis that the final decision to begin smoltification may begin well into the spring. Skilbrei (1988) has also suggested that Atlantic salmon may begin to smoltify early in the spring. Studies which have indicated that juvenile Atlantic salmon must reach a critical length in the fall in order to smoltify the following spring (Elson 1957; Thorpe et al. 1980) may reflect poor winter growing conditions for Atlantic salmon. Thus, the size which fish are able to reach in the early spring may be largely dictated by the size they are able to achieve the previous growing season. In corroboration with the results of Kristinsson et al. (1985), Skilbrei (1988) and Stefansson et al. (1989), Atlantic salmon in this study, growing in water that remained near 10°C, appeared to be recruited continually into an UMG as smolts.

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ABSTRACTS OF PAPERS

Social Dynamics in Salmonid Fishes: Do Kin Make Better Neighbours?

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Kin discrimination has been reported in a number of animal taxa, including fishes, however, functional explanations for this ability have not been examined. In this study, we used two species of salmonids which have been shown to discriminate between kin and non-kin. Using groups of full sibling and unrelated juvenile Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) in an artificial stream tank, we determined whether kin discrimination has an effect on the territorial dynamics in these fishes. The form and frequency of agonistic interactions, and the mean distance to nearest neighbours were observed. Mean frequency of agonistic interactions was found to be significantly higher in non-kin groups of either species when compared to kin groups, and mean distance to nearest neighbour was significantly lower in kin groups for both species. In addition, kin groups utilized a significantly lower proportion of 'overtly aggressive' territorial defence behaviours and a significantly higher proportion of 'passive' territorial defence behaviours compared to non-kin in both species. These results suggest that inclusive fitness benefits may be associated with maintaining territories near kin versus non-kin conspecifics.

La discrimination par la parenté a été signalée chez un certain nombre de taxons animaux, y compris les poissons, mais les explications fonctionnelles de cette aptitude n'ont pas été examinées. Dans notre étude, nous avons utilisé deux espèces de salmonidés chez qui on a montré une discrimination entre la parenté et l'absence de parenté. En nous servant de groupes de juvéniles germains et sans lien de parenté de saumon atlantique (*Salmo salar*) et de truite arc-en-ciel (*Oncorhynchus mykiss*) dans un bassin créant un cours d'eau artificiel, nous avons déterminé si la discrimination par la parenté a un effet sur la territorialité chez ces poissons. Nous avons observé la forme et la fréquence des interactions agonistiques, et la distance moyenne par rapport aux voisins les plus proches. La fréquence moyenne des interactions agonistiques est apparue nettement plus élevée dans les groupes sans lien de parenté, chez les deux espèces, par rapport aux groupes apparentés, et la distance moyenne par rapport aux voisins les plus proches était nettement plus basse dans les groupes apparentés chez les deux espèces. De plus, les groupes apparentés utilisaient une proportion nettement plus faible de comportements de défense territoriale « ouvertement agressifs » et une proportion nettement plus élevée de comportements de défense territoriale « passifs » par rapport aux groupes non apparentés chez les deux espèces. Ces résultats semblent indiquer qu'il peut être profitable sur le plan de la santé de maintenir un territoire à proximité de congénères apparentés plutôt que non apparentés.

Length of Age 1+ Salmon Parr Indicates Stock Status

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Because it is expensive to count smolts and difficult to account for habitat heterogeneity in electrofishing surveys, growth of juveniles or recruits is often more easily measured than abundance. A review of data from Western Arm Brook and Big Salmon, Margaree, Miramichi, Restigouche, and Little Codroy rivers indicated that size of parr and smolts was inversely correlated to stock abundance. Length of age 1+ parr was the most sensitive indicator of stock abundance and could be described by an inverse logistic curve. It was hypothesized that mean size of age 1+ parr would decline when spawning requirements were exceeded.

Étant donné qu'il est coûteux de dénombrer les smolts et difficile de rendre compte de l'hétérogénéité des habitats dans les relevés à la pêche électrique, il est souvent plus facile de mesurer la croissance des juvéniles ou des recrues que l'abondance. Un examen des données recueillies dans le ruisseau Western Arm et dans les rivières Big Salmon, Margaree, Miramichi, Restigouche et Little Codroy a indiqué que la taille des tacons et des smolts était inversement corrélée à l'abondance du stock. La longueur des tacons d'âge 1+ était l'indicateur le plus sensible de l'abondance du stock et pouvait être décrite par une courbe logistique inverse. On pose pour hypothèse que la taille moyenne des tacons d'âge 1+ baisserait lorsque les besoins de la reproduction seraient dépassés.

Seasonal Influence and Metabolic Strategies Demonstrated by Juvenile Atlantic Salmon (*Salmo salar*)

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The relationship between seasonal habitat shifts by juvenile Atlantic salmon in freshwater and their physiological state was examined by measuring current holding ability and by studying metabolic differences at differing seasonal temperatures.

The critical holding velocity (CHV) was measured during the first year of freshwater residence for two different developmental strategies of juvenile Atlantic salmon (fast- and slow-growing), and during the second year of freshwater residence for the slower-growing parr. The main findings are as follows: i) For both strategies CHV decreased with decreasing temperature. ii) In absolute terms (cm per s) the CHV of the faster-growing group remained consistently higher than that of the slower-growing group until May. iii) In relative terms (body lengths per s) there was no difference between groups until the faster-growing group showed signs of smolting in May. At this time the CHV of the slower-growing group increased with temperature, whereas that of the faster-growing fish remained at a low level. iv) The CHV profiles for the slower-growing group during their second year of freshwater residence (i.e. prior to smolting) showed the same pattern of temperature sensitivity as the faster-growing group during their first year in freshwater.

Changes in seasonal metabolism were related to different strategies adopted by salmon parr. The role of possible isoenzymes involved in lipid synthesis (Glucose-6-phosphate dehydrogenase) and anaerobic muscle contraction (lactate dehydrogenase) was investigated by measuring Km and Vmax at different temperatures. The results were as follows: i) Both enzymes tended to be most efficient at the temperature ambient when the fish were sampled. ii) This relationship broke down, however, during smolting. iii) There was no difference between the two groups of fish in the efficiency of LDH. iv) During winter and spring the G6PDH of the slower-growing fish was more efficient than that of the faster-growing fish.

In conclusion, juvenile salmon appear to acclimatize biochemically to seasonal temperatures, and there are differences between the different life-history strategies that may be linked with their differing ecologies.

Nous avons examiné la relation entre les changements saisonniers d'habitat chez les juvéniles de saumon atlantique en eau douce et leur état physiologique en mesurant l'aptitude à se maintenir dans le courant et en étudiant les différences métaboliques à diverses températures saisonnières.

La vitesse critique de maintien (CHV) a été mesurée pendant la première année de résidence en eau douce pour deux stratégies différentes de développement chez les juvéniles de saumon atlantique (croissance rapide et croissance lente) et pendant la deuxième année de résidence en eau douce pour les tacons à croissance lente. Les principaux résultats sont les suivants : i) Pour les deux stratégies, la CHV baissait en même temps que la température. ii) En termes absolus (cm par sec), la CHV du groupe à croissance rapide restait régulièrement plus élevée que celle du groupe à croissance plus lente jusqu'en mai. iii) En termes relatifs (longueur corporelle par sec), il n'y avait pas de différence entre les groupes jusqu'à ce que le groupe à croissance rapide montre en mai des signes de smoltification. À ce moment-là, la CHV du groupe à croissance lente a augmenté avec la température, tandis que celle des poissons en cours de smoltification restait à un niveau bas. iv) Les profils de la CHV pour le groupe à croissance lente pendant la deuxième année de résidence en eau douce (c.-à-d. avant la smoltification) montraient le même patron de sensibilité à la température que le groupe à croissance rapide pendant sa première année en eau douce.

Les changements dans le métabolisme saisonnier ont été mis en rapport avec différentes stratégies adoptées par les tacons. Le rôle possible des isœnzymes qui entrent dans la synthèse des lipides (glucose-6-phosphate déshydrogénase) et dans la contraction anaérobie des muscles (lactate déshydrogénase) a été examiné par la mesure de Km et de Vmax à différentes températures. Les résultats obtenus sont les suivants : i) Les deux enzymes semblaient être les plus efficaces aux températures ambiantes que connaissaient les poissons au moment de l'échantillonnage. ii) Cette relation a toutefois disparu pendant la smoltification. iii) Il n'y avait pas de différence entre les deux groupes de poissons en ce qui concerne l'efficacité de la LDH. iv) Pendant l'hiver et le printemps, la G6PDH des poissons à croissance lente était plus efficace que celle des poissons à croissance rapide.

En conclusion, les saumons juvéniles semblent s'acclimater biochimiquement aux températures saisonnières, et il y a des différences dans les stratégies du cycle biologique qui peuvent être liées à des différences d'ordre écologique.

Habitat Improvement in a Large Norwegian Salmon Stream

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The lower sections of many large streams support low pre-smolt densities of Atlantic salmon and brown trout. The main reasons seem to be bottom substratum dominated by sand and fine gravel. An experimental area in the River Gaula, Central Norway, was established to analyze production of juveniles. Densities and movements of presmolts were analyzed in relation to bottom substratum and water velocity. Results indicate that the production of salmonids can be significantly improved by adjusting the bottom substratum to an optimal size.

Le cours inférieur de nombreux grands cours d'eau abrite des densités faibles de pré-smolts de saumon atlantique et de truite brune. Les principales raisons semblent en être le substrat du fond, dominé par le sable et le gravier fin. Pour analyser la production de juvéniles, on a créé une zone expérimentale dans la rivière Gaula, au centre de la Norvège. Les densités et les déplacements des pré-smolts ont été analysés en fonction du substrat du fond et de la vitesse de l'eau. Les résultats indiquent que la production de salmonidés peut être nettement améliorée si l'on modifie le substrat du fond pour lui donner la granulométrie optimale.

Aspects of Natural Hybridization Between Atlantic Salmon and Brown Trout: Molecular Biochemistry in Population Ecology

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Possible causes of widespread natural hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in Newfoundland were investigated. Allozyme electrophoresis was used to identify hybrid fish and estimate frequencies of hybridization within nine river systems. Mitochondrial DNA analysis using the 'polymerase chain reaction' (PCR) and direct nucleotide sequencing was used to determine the maternal and paternal species of each hybrid. Also, controlled breeding experiments were performed to compare the viability of reciprocal crosses and purebred lines.

In total, 37 hybrid fish were identified with hybridization frequencies ranging between 0.0 to 18.7% in the rivers. No relationship was apparent between the rate of hybridization and the abundance of each of the species relative to the other. All hybrid fish had brown trout mothers. In breeding experiments, a cross with salmon milt fertilizing brown trout eggs showed relatively low viability compared to the reciprocal cross. These results suggest that hybridization between the two species in Newfoundland rivers is unidirectional, between male Atlantic salmon and female brown trout. A likely explanation for this is that sexually mature male salmon parr are 'sneaking' copulations with brown trout females.

Nous avons examiné les causes possibles du phénomène répandu de croisement naturel entre le saumon atlantique (*Salmo salar*) et la truite brune (*S. trutta*) à Terre-Neuve. L'électrophorèse des allozymes nous a permis d'identifier les hybrides et d'estimer la fréquence des croisements dans neuf réseaux hydrographiques. L'analyse de l'ADN mitochondrial à l'aide de la «réaction en chaîne de la polymérase» (PCR) et du séquençage direct des nucléotides a servi à déterminer l'espèce des géniteurs mâle et femelle de chaque hybride. De plus, nous avons effectué des expériences de croisement contrôlé pour comparer la viabilité des hybridations dans les deux sens et des lignées pures.

Au total, on a identifié 37 hybrides, avec des fréquences de croisement allant de 0,0 à 18,7 % dans les divers cours d'eau. On n'a mis en évidence aucune relation entre le taux de croisement et l'abondance relative des deux espèces. Tous les hybrides recueillis avaient pour mères des truites brunes. Dans les expériences d'élevage, ce croisement, avec laitance de saumon fécondant des œufs de truite brune, présentait une viabilité relativement faible par rapport au croisement inverse. Ces résultats semblent indiquer que les événements de croisement entre ces espèces dans les cours d'eau de Terre-Neuve sont unidirectionnels, les mâles de saumon atlantique fécondant toujours des femelles de truite brune. On peut vraisemblablement expliquer ce phénomène par l'activité de tacons mâles de saumon sexuellement mature qui « se faufilent » pour copuler avec des truites brunes femelles.

Assessing Genetic Variation within Atlantic Salmon Populations using PCR

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Much discussion has taken place on the extent of genetic variation within the species of Atlantic salmon (*Salmo salar* L.). A relatively new technique, the automation of the Polymerase Chain Reaction (PCR) permits generation of multiple copies of specific regions of DNA. This DNA may then be directly sequenced, permitting inter- and intrapopulation comparisons. A major advantage of this method over conventional techniques such as morphological, allozyme or restriction fragment analyses, is the requirement of minute amounts of tissue or blood (µg or µL quantities are sufficient).

In the present study Atlantic salmon (*Salmo salar*) from North America and from Europe were examined to assess the potential of PCR and sequence analysis in determining levels of intraspecific variation. The mitochondrial gene, cytochrome b, was chosen for this initial investigation. Three genotypes were evident; these differed from each other at two out of 300 base positions, both representing silent codon changes. One genotype only was found in the European sample whereas all three genotypes were present in the North American sample.

L'importance de la variation génétique du saumon atlantique (*Salmo salar* L.) suscite un débat animé. Une technique relativement nouvelle, l'automatisation de la réaction en chaîne de la polymérase (PCR) permet de générer des copies multiples de régions spécifiques de l'ADN. Il est ensuite possible de séquencer directement cet ADN et de faire des comparaisons inter- et intra-populations. Le grand avantage de cette méthode par rapport aux techniques conventionnelles comme l'analyse morphologique et l'analyse des allozymes ou des fragments de restriction est le fait qu'il suffit d'une quantité infime de tissus ou de sang (une quantité de l'ordre du µg ou du µL suffit).

Dans la présente étude, nous avons examiné *S. salar* d'Amérique du Nord et d'Europe en vue d'évaluer le potentiel de la PCR et de l'analyse séquentielle pour déterminer l'importance de la variation intra-spécifique. On a choisi pour cette étude préliminaire le gène mitochondrial qui encode le cytochrome b. Nous avons observé trois génotypes, qui différaient les uns des autres à deux bases sur 300, ce qui représentait dans les deux cas des changements non exprimés du codon. Un seul génotype était présent dans l'échantillon européen, tandis que les trois ont été observés dans l'échantillon nord-américain.

Fall-Fingerling Atlantic Salmon Released to Natural Lacustrine Nursery Areas in Newfoundland, Canada[1]

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Controlled releases of fall-fingerling Atlantic salmon (*Salmo salar*) into salmon-free lacustrine habitats in Newfoundland resulted in average survival from parr to smolt, in three consecutive annual releases, of 12.9%. Year-class survival decreased progressively with consecutive releases. Juvenile salmon biomass from lacustrine habitat remained relatively stable over the duration of the study, suggesting that the average annual biomass of 1.6 $kg \cdot ha^{-1}$ of juvenile salmon released to lacustrine habitat did not exceed habitat carrying capacity. Male precocity was observed but did not appear to represent a significant deterrent to fall-fingerling survival. Annual smolt yield (by year-class) from stocking ranged from 53 to $130 \cdot ha^{-1}$ (mean = 77 $smolts \cdot ha^{-1}$).

Historical data on the salmon source stock, indicate that smolts of riverine origin (i.e. prior to implementation of lacustrine experiments) were 10% age 2, 75% age 3, 15% age 4. Brood salmon returning to Indian Brook from historical riverine salmon year classes were, 2.1% from age 2 smolts, 57% from age 3 smolts and 40% from age 4 smolts. Smolt emigration from lacustrine nursery areas has resulted in a progressive shift in the age at smoltification of lacustine smolts relative to that of the parent Indian Brook stock. By 1989, smolt age composition had shifted to 21% age 2, 70% age 3 and 9% age 4.

Les libérations contrôlées d'alevins d'automne de saumon atlantique (*Salmo salar*) dans des habitats lacustres de Terre-Neuve ont donné une survie moyenne du tacon au smolt, sur trois années consécutives de libération, de 12,9 %. La survie de la classe annuelle décroissait progressivement d'une année à l'autre. Le taux d'augmentation de la biomasse de saumons juvéniles provenant des habitats lacustres est resté relativement stable pendant la durée de l'étude, ce qui peut indiquer que la biomasse moyenne annuelle de 1,6 $kg \cdot ha^{-1}$ de saumons juvéniles libérés dans un habitat lacustre naturel ne dépassait pas la capacité de port de cet habitat. On a observé de la précocité chez les mâles, mais cela ne semblait pas représenter un obstacle important à la survie des alevins de l'automne. La production annuelle de smolts (par classe annuelle) provenant de l'ensemencement allait de 53 à $130 \cdot ha^{-1}$ (moyenne = 77 $smolts \cdot ha^{-1}$).

Les données historiques sur le stock de saumons dont provenaient les juvéniles servant à l'ensemencement lacustre indiquent que les smolts d'origine lotique (c.-à-d. avant le début des expériences en lac) étaient à 10 % d'âge 2, à 75 % d'âge 3, à 15 % d'âge 4. Parmi les géniteurs qui retournaient au ruisseau Indian et appartenaient aux classes annuelles des saumons d'origine lotique, 2,1 % provenaient de smolts d'âge 2, 57 % de smolts d'âge 3 et 40 % de smolts d'âge 4. L'émigration des smolts des nourriceries lacustres a causé un changement progressif de l'âge à la smoltification chez les smolts de lac par rapport à celui des géniteurs du ruisseau Indian. En 1989, l'âge des smolts s'était modifié : 21 % d'âge 2, 70 % d'âge 3 et 9 % d'âge 4.

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[1] This poster material was presented originally to the symposium on "The Dynamics and Use of Lacustrine Ecosystems" in Helsinki, Finland. The original paper is in press (Hydrobiologia 1-11, 1992).

Distribution of Fish in Three Coastal Watersheds of New Brunswick and Nova Scotia, Canada

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Environmental factors influencing assemblages of fish were investigated in the St. Croix (NB), Gold and Medway (NS) stream systems. Stream size-related variables (discharge, median summer temperature) and alkalinity-related variables (alkalinity, pH, calcium, DOC, AL) were the two classes of variables influencing species composition and richness, as determined by discriminant function analysis of TWINSPAN classes. In the circumneutral St. Croix watershed, creek chub (*Semotilus atromaculatus*), brook trout (*Salvelinus fontinalis*), blacknose dace (*Rhinichthys atratulus*), Atlantic salmon (*Salmo salar*), eel (*Anguilla rostrata*) and fallfish (*Semotilus corporalis*) dominated stream sites of progressively greater discharge and higher median mid-summer temperature. In the acidic Gold watershed, the brook trout, salmon and eel exhibited a distribution pattern in relation to stream size similar to that for the St. Croix, with the eel relatively more abundant at large stream sites. The creek chub was excluded from the smallest tributaries by low pH. In the slightly more acidic Medway system, relative abundance of Atlantic salmon is reduced and that of eel increased, compared to the Gold and St. Croix systems. The geographic distributions of blacknose dace and fallfish do not extend to southwestern Nova Scotia. The midsummer pH levels limiting the creek chub, salmon, brook trout and eel were 5.2, 5.0, 4.7 and <4.5, respectively.

Nous avons examiné les facteurs environnementaux qui influent sur les assemblages de poissons dans les réseaux de la rivière Sainte-Croix (N.-B.) et des rivières Gold et Medway (N.-É.). Les variables liées à la taille du cours d'eau (débit, température estivale moyenne) et les variables liées à l'alcalinité (alcalinité, pH, calcium, COD, AL) étaient les deux classes de variables qui avaient un effet sur la composition et la richesse spécifiques, après analyse discriminante des classes TWINSPAN. Dans le réseau presque neutre de la Sainte-Croix, le mulet à cornes (*Semotilus atromaculatus*), l'omble de fontaine (*Salvelinus fontinalis*), le naseux noir (*Rhinichthys atratulus*), le saumon atlantique (*Salmo salar*), l'anguille (*Anguilla rostrata*) et la ouitouche (*Semotilus corporalis*) dominaient les sites où on observait une augmentation progressive du débit et de la température moyenne au milieu de l'été. Dans le bassin acide de la rivière Gold, l'omble de fontaine, le saumon et l'anguille présentaient un schéma de distribution par rapport à la taille du cours d'eau similaire à celui de la Sainte-Croix, l'anguille étant relativement plus abondante aux sites établis dans les cours d'eau les plus gros. Le mulet à cornes était exclu des plus petits affluents à cause du pH bas. Dans le réseau légèrement plus acide de la Medway, l'abondance relative du saumon atlantique est réduite et celle de l'anguille augmente par rapport aux réseaux de la Gold et de la Sainte-Croix. La distribution géographique du naseux noir et de la ouitouche ne s'étendait pas jusqu'au sud-ouest de la Nouvelle-Écosse. Les niveaux limitants du pH au milieu de l'été pour le mulet à cornes, le saumon, l'omble de fontaine et l'anguille étaient respectivement de 5, 2, 5,0, 4,7 et <4,5.

A New Imaging Technique for Automated Fish Counting, Measuring, and Data Collection

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High contrast, silhouette images of fish can be made as they pass through a specially designed tunnel and lighting system. Simultaneous side and top views of migrating fish are created by directly photographing the view through the near-transparent side wall of the tunnel while the top view is created simultaneously through an angled mirror mounted directly above the transparent top wall of the tunnel. Both the far and bottom walls of the tunnel are coated with retroreflective material, and retroreflective lighting, commonly experienced when viewing traffic signs at night, is used to produce the desired illumination effects; any object between the retroreflector and the light source will appear to the observer as a silhouette. To apply this concept to photography of migrating fish, a semi-transparent mirror, or beam-splitter, is placed in front of a closed-circuit television camera and a light is reflected toward the retroreflective surfaces of the tunnel in direct line with the optical axis of the camera; this placement ensures maximum brightness of the background, and maximum contrast between the background and the darker silhouette image of the fish. The resulting stereo view enables accurate calculation of the distance between the camera and the fish, which in turn enables calibration of the system for accurate estimates of fish measurements. The top view also enables separation of images of two or more fish which may be swimming in close proximity in the tunnel.

High contrast images in water which is too dirty or coloured for normal underwater photography are possible. The tunnel is mounted in a box covered with transparent blue material which blocks out red light from the sun, while the camera is fitted with a red filter which blocks the blue light from the sun; this filtering system allows the tunnel to be well lit during the day although it effectively blocks all ambient sunlight from the camera and enables total control of lighting through use of artifical lighting. The exceptionally high light-gathering efficiency of the system enables remote operation with 12-volt car batteries while the coloured filters enable 24-hour operation.

The high quality silhouette images were ideal for machine vision as they required very little image enhancement prior to computer analysis. A computer equipped with an image-processing board and specially-designed software was able to automatically count and measure migrating fish in real time.

Il est possible d'obtenir des silhouettes très contrastées des poissons quand ils passent dans un tunnel aménagé avec un dispositif d'éclairage spécialement conçu. On crée simultanément une vue latérale et une vue d'en haut des poissons en migration en photographiant directement la vue latérale à travers la paroi presque transparente du tunnel tout en créant la vue d'en haut grâce à un miroir incliné monté juste au-dessus de la paroi supérieure transparente du tunnel. Le fond et le mur arrière du tunnel sont recouverts de matériau rétroréfléchissant, et un éclairage rétroréfléchissant (ce qu'on observe la nuit quand on regarde les panneaux de signalisation) sert à produire les effets d'éclairement désirés; tout objet placé entre le rétroréflecteur et la source de lumière apparaîtra à l'observation comme une silhouette. Pour appliquer ce concept à la photographie des poissons en migration, on place un miroir semi-transparent, ou séparateur de faisceau, devant une caméra de télévision en circuit fermé, et un faisceau de lumière est réfléchi par lui vers les surfaces rétroréfléchissantes du tunnel, et en ligne droite de l'axe optique de la caméra; cela donne un maximum de brillance au fond, et un contraste maximum entre le fond et la silhouette plus sombre du poisson. La vue stéréoscopique qui en résulte permet de calculer précisément la distance entre la caméra et le poisson, ce qui permet ensuite d'étalonner le système pour avoir des estimations exactes des mesures. La vue d'en haut permet aussi de séparer les images de deux ou plusieurs poissons qui peuvent avancer en se tenant très près l'un de l'autre dans le tunnel.

Il est possible d'obtenir des images très contrastées dans de l'eau qui est trop sale ou colorée pour permettre de la photographie normale sous l'eau. Le tunnel est installé dans une boîte couverte d'un matériau bleu transparent qui bloque le rayonnement rouge du soleil, tandis que la caméra est équipée d'un filtre rouge qui bloque le rayonnement bleu du soleil; ce système de filtre permet de garder le tunnel bien éclairé pendant la journée tout en empêchant efficacement la lumière solaire ambiante d'atteindre la caméra, et permet de contrôler totalement l'éclairage à l'aide de lumière artificielle. L'efficacité exceptionnelle du système pour le captage de la lumière permet le travail à distance avec des batteries d'automobile de 12 volts, tandis que la combinaison de filtres colorés permet de travailler soit le jour soit la nuit.

La grande qualité des silhouettes produites convient idéalement à la vision artificielle, car les images demandent très peu d'amélioration avant l'analyse par ordinateur. Un ordinateur équipé d'une unité de traitement d'images et d'un logiciel spécialement conçu a pu compter et mesurer automatiquement en temps réel les saumons en migration.

Phenotypic Diversity of Atlantic Salmon (*Salmo salar*) Juveniles in Little Codroy River (Southwest Newfoundland)

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Phenotypic diversity of Atlantic salmon (*Salmo salar*) 1+ parr was analyzed according to size, growth, condition, sex and maturation in Little Codroy River (southwest Newfoundland). Effects of four factors, i.e. geographical zone, year, density of parr and physical habitat, were assessed and discussed. Zone effect was most important. Patterns in year effect were similar for every part of the mainstem, whereas they differed between tributaries. Density influenced the biological characteristics of 1+ parr in tributaries. The effect of physical habitat seemed to be weak. Even within a small system like the Little Codroy, we observed an important heterogeneity in time and space in the 1+ parr population.

La diversité phénotypique des tacons 1+ de saumon atlantique (*Salmo salar*) a été analysée selon la taille, la croissance, la condition, le sexe et le degré de maturation dans la rivière Little Codroy (sud-ouest de Terre-Neuve). Les effets de quatre facteurs (zone géographique, année, densité des tacons et habitat physique) ont été évalués et analysés. L'effet de la zone était le plus important. Les patrons de l'effet de l'année étaient très similaires pour toutes les parties de l'axe fluvial, tandis qu'ils différaient d'un affluent à l'autre. La densité influait sur les caractéristiques des tacons 1+ dans les affluents. L'effet de l'habitat physique semblait faible. Malgré la petite taille du système de la Little Codroy, nous avons observé une forte hétérogénéité spatio-temporelle dans la population de tacons 1+.

High Quality Salmonid Waters in an Urban Environment

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Exceptionally high densities of brown trout (*Salmo trutta* L.), with biomass up to 53 $g \cdot m^{-2}$, occur in the city rivers of St. John's, Newfoundland. The enhanced biomass may be due to: relatively high levels of nutrients, stimulating primary production; relatively high pH and suitable water chemistry, thereby enhancing breakdown of organic detritus; and sufficient gradient allowing good riffle and pool type habitat with a coarse substrate. Therefore abundant invertebrates suitable as food organisms are available, and habitat suitable for trout is present. Piscine competitors and predators are uncommon similar to other waters of the island. Headwater wetlands and a wet climate provide stable water flows. Except in some downstream sections of the city rivers, industrial pollutants do not limit fish production. In contrast to many other urban rivers, urbanization appears to have enhanced salmonid production, although changes in stream morphology and temperature may have given the introduced brown trout the competitive advantage over the native brook trout *Salvelinus fontinalis* (Mitchill), which is now common only in cool boggy headwaters, or above obstructions. Unfortunately, development is now proceeding in headwater areas, where governmental guidelines concerning conservation of buffer strips and wetlands, installation of storm sewers, etc., are generally ignored. Trout stocks in these areas are deteriorating, and downstream areas will inevitably be affected if poor practices in development continue.

Des densités et une biomasse exceptionnellement élevées, de l'ordre de 53 $g \cdot m^{-2}$, de truite brune (*Salmo trutta* L.) sont observées dans les cours d'eau de la ville de St. John's, à Terre-Neuve. La hausse de la biomasse peut être due à des niveaux relativement élevés de nutriants, qui stimulent la production primaire, à un pH relativement élevé et des caractéristiques chimiques de l'eau bien adaptées qui accélèrent la dégradation des détritus organiques, et enfin à une dénivellation suffisante qui permet la présence d'un bon habitat de radiers et de fosses avec un substrat grossier, de sorte qu'il existe une abondance d'invertébrés pouvant servir pour la nourriture, et que l'habitat convient à la truite. En outre, comme dans d'autres eaux de l'île, il y a peu de poissons concurrents et de prédateurs. La présence de terres humides dans le cours supérieur et le climat humide assurent la stabilité des apports hydriques. Sauf dans certaines portions d'aval, les polluants industriels ne limitent pas la production de poissons. Contrairement à ce qu'on observe dans d'autres régions, l'urbanisation semble avoir stimulé la production de salmonidés, mais des changements dans la morphologie et la température des cours d'eau peuvent avoir donné à la truite brune, espèce introduite, un avantage sur l'espèce indigène, l'omble de fontaine *Salvelinus fontinalis* (Mitchill), qui n'est maintenant commune que dans les eaux froides et marécageuses du cours supérieur, où au-dessus des obstacles. Malheureusement, on observe maintenant un développement dans le cours supérieur, où les lignes directrices gouvernementales sur la conservation de bandes tampons et de terres humides, l'installation d'égouts pluviaux, etc., sont généralement ignorées. Dans ces régions, les stocks de truites se détériorent, et les zones d'aval seront aussi affectées si le développement se poursuit de la même façon.

Genetic Variation, Habitat Diversity, and Production of Juvenile Salmonids in Freshwater

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During the life cycle of anadromous salmonids, mortality rate is typically greatest during the juvenile freshwater residence stage. There is, therefore, ample opportunity for natural selection to influence the distribution of genetically determined traits influencing survival of juvenile fish in freshwater. Habitat diversity, as measured by the range of abiotic and biotic environmental conditions encountered by members of a population in freshwater, is considered as an important selective factor promoting genetic variation within and between populations. Such genetic variation is important, both for promoting adaptation to changing environmental conditions, hence influencing production within local populations, and for promoting adaptive diversification and influencing fish production among local populations. Quantitative and qualitative examples illustrate genetic variation which is apparently maintained by different manifestations of habitat diversity in stream fishes. It is argued that detailing the extent and maintenance of ecological-genetic variation in salmonid populations is crucial to an understanding of variation in fish production in natural freshwaters. Rapidly developing molecular genetic techniques have many applications in population biology and examples are given showing how these techniques can promote understanding of genetic factors which influence production of juvenile salmonids in freshwater.

Pendant le cycle biologique des salmonidés anadromes, le taux de mortalité est généralement au maximum pendant le stade juvénile de résidence en eau douce. Il y a donc largement place pour la sélection naturelle qui influe sur la distribution de traits déterminés génétiquement qui ont un effet sur la survie des juvéniles en eau douce. La diversité des habitats, mesurée par la gamme de conditions environnementales biotiques et abiotiques que connaissent les membres d'une population en eau douce, est considérée comme un important facteur de sélection qui stimule la variation génétique dans une population et entre les populations. Cette variation génétique est importante tant pour promouvoir l'adaptation à des conditions environnementales changeantes, et donc influer sur la production au sein de populations locales, que pour promouvoir la diversification adaptative et influer sur la production de poissons parmi les populations locales. Les exemples donnés illustrent la variation génétique quantitative et qualitative qui semble maintenue par différentes manifestations de la diversité des habitats chez les poissons des cours d'eau. Nous soutenons qu'une étude détaillée de l'étendue et du maintien de la variation écologico-génétique chez les populations de salmonidés est essentielle à la compréhension de la variation de la production de poissons dans les eaux douces naturelles. Les techniques de pointe du génie moléculaire ont de nombreuses applications dans la biologie des populations, et les exemples donnés montrent que ces techniques peuvent permettre de mieux comprendre les facteurs génétiques qui influent sur la production des salmonidés juvéniles en eau douce.

APPENDIX
List of Participants and Referees

Participants

Amiro, P.G.
Anderson, J.M.
Baglinière, J.-L.
Bain, L.H.
Beland, K.F.
Bourgeois, C.E.
Bridcut, E.E.
Brown, G.E.
Brown, J.A.
Bustard, D.R.
Caron, F.
Chadwick, E.M.P.
Chaput, G.J.
Cunjak, R.A.
Cutting, R.E.
Dempson, J.B.
Desjardine, R.L.
Donnelly, W.A.
Elliott, J.M.
Fryer, J.K.
Gephard, S.
Gibson, R.J.
Goosney, R.F.
Gotceitas, V.
Graham, W.D.
Grant, J.W.A.
Green, J.M.
Heggberget, T.G.
Hooper, W.C.
Houston, K.
Hutchinson, P.
Hvidsten, N.A.
Jones, M.L.
Karlström, Ö.
Kennedy, G.J.A.
Kerr, H.
Le Drew, L.J.
Lessard, M.
McGowan, C.
McKinley, R.S.
McVeigh, H.P.
Mills, S.
Morgan, J.
Myers, R.A.
Nicieza, A.G.

Participants (Cont.)

O'Brien, J.O.
O'Connell, M.F.
Orr, D.
Patrick, P.H.
Pepper, V.A
Pippy, J.H.C.
Porter, T.R.
Power, G.
Power, M.
Pratt, J.D.
Prevost, E.
Raat, A.J.P.
Reddin, D.G.
Richardson, J.S.
Roberge, M.
Ryan, P.M.
Scott, A.
Scruton, D.A.
Short, B.P.
Seiler, D.
Stansbury, D.E.
Steele, D.M.
Talbot, A.
Taylor, E.B.
Tremblay, G.
Ward, B.R.
Waters, T.F.
Whitaker, R.
Whitesel, T.A.
Williams, U.P.
Winstone, A.

Referees

Abrahams, M.
Barton, D.R.
Beland, K.F.
Bohlin, T.
Bowlby, J.N.
Chadwick, E.M.P.
Coad, B.W.
Colgan, P.W.
Cunjak, R.A.
Cutting, R.E.
D'Amours, P.
Dempson, J.B.
Dunbrack, R.L.
Duston, J.
Fausch, K.D.
Gaudin, P.
Haedrich, R.L.
Hearn, W.E.
Heggenes, J.
Holtby, L.B.
Hunt, R.L.
Huntingford, F.A.
Jessop, B.M.
Keenleyside, M.H.A.
Landry, G.
Larson, D.J.
Morantz, D.L.
Morgan, J.
Noakes,D.L.G.
Northcote, T.G.
O'Connell, M.F.
Pepin, P.
Peterson, R.H.
Randall, R.G.
Ringler, N.H.
Ritter, J.A.
Saunders, R.L.
Shelton, P.
Shirvell, C.S.
Steele, D.H,
Waters, T.F.
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White, W.J.
Williams, D.D.

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